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Seed morphology of Australian species of *Nymphoides* (Menyanthaceae)

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Abstract

Seeds of all known Australian species of *Nymphoides* have been examined externally and measured by light microscope. Representative seeds were selected, and their micromorphology examined by Scanning Electron Microscope (SEM). The results indicate that a combination of seed size, shape, ornamentation and caruncle is distinctive for most species when ornamentation is developed to its fullest extent. However the fullest degree of ornamentation for many species may be reduced or absent even in mature seeds, and sometimes within the same population. Fully ornamented seeds and known variations are described and illustrated. Immature seeds should not be used for comparisons.

Introduction

This work on seeds was undertaken as part of my long-term interest in morphological revisionary studies on the taxonomy of *Nymphoides* within Australia, involving both herbarium and field observations.

The taxonomic value of seed size, shape, ornamentation, and of any caruncular excrescence in Menyanthaceae has been widely recognised. This value is at species level, with well-developed seeds being diagnostic for most species. Botanical drawings in many accounts of Menyanthaceae taxa include seed illustrations from light microscopy (e.g. Aston 1969, 1982, 1984, 1986, 1987, 1997; Raynal 1974; Short 2000) but some SEM studies have been used also (Sivarajan et al. 1989; Chuang & Ornduff 1992).

Seed morphology and its bearing on the systematics of the five genera in Menyanthaceae have been discussed by Chuang and Ornduff (1992). From their work, they concluded that it would not be possible to define any unique set of seed morphological or cellular characters that would distinguish either Menyanthaceae at family level or any of its contained taxa at generic level. However, the high diversity in seed morphology provided ready distinctions between species.

The SEM studies of Chuang and Ornduff (1992) embraced representative seeds of all five genera in the Menyanthaceae, three of which occur in Australia. The studies included the monotypic *Liparophyllum* (sample from New Zealand, but the species is also native in Tasmania), fourteen species of *Villarsia* (1 South African; all 13 Australian species), and six species of *Nymphoides* from different continents (with *N. exigua* from Tasmania). The current study provides descriptions and SEM illustrations of seeds of all 20 species of *Nymphoides* known from Australia, with discussion on the consistency or variation of seed ornamentation in each species. It compliments and expands the work of Chuang and Ornduff in relation to Australian taxa so that data from seed samples of all species of Menyanthaceae known to occur in Australia are now available.

Materials and Methods

Seeds from the several hundred collections housed in all major Australian herbaria, and some from extra-Australian herbaria and localities, were first examined under magnifications of up to 50 times natural size, using a dissecting microscope fitted with a measuring graticule. This allowed seeds to be measured and representative seeds to be

selected for SEM examination. Within each species, seeds were chosen to indicate the kind or kinds of ornamentation, the maximum size and density of tubercles when present, any variation in the kinds of tubercles present or in their size or development, and variation due to seed immaturity. Seeds were also selected to demonstrate geographical variation, including some relevant examples from the extra-Australian range of some species. Collections from which seeds were examined by SEM are detailed in Appendix 1.

SEM examination and photography has been done using the facilities of the Jodrell Laboratory, Royal Botanic Gardens, Kew, England during 1973-1974, the Department of Botany, Monash University, Melbourne in 1989, and the School of Botany, University of Melbourne during 2000-2001.

Results

The number of collections of each species examined by light microscopy, excluding collections without seeds, and the number of those used for SEM samples are given below against each species name (see also Appendix 1). Appendix 2 lists all collections cited in this paper, whether in the main text or in Appendix 1, and indicates the identification of each collection.

In the seed description for each species, seeds with the "peak" or most highly developed ornamentation, or ornamentations, found on mature seeds are described first under the heading of "peak ornamentation". An account of any morphological and/or geographical variations seen is given next under a second heading "variation".

The term "seed body" refers to the whole seed excluding any caruncle, scale, or tubercles. Measurement of the seed body alone allows for consistent comparisons of seed size within species which have seeds which may be either smooth or tuberculate, and between species with differing tuberculate structures.

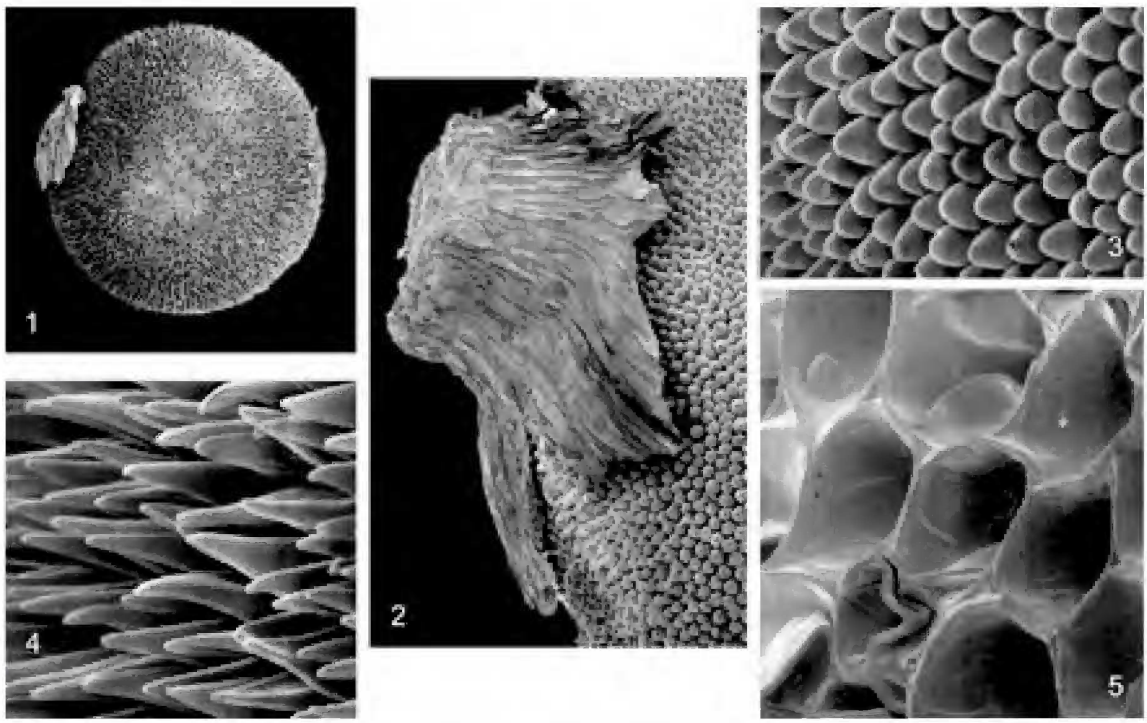
The term "periclinal walls" refers to the visible, i.e. the surface walls of the epidermal cells of the seed. The margins of these walls are most frequently pentagonal and hexagonal (e.g. figs 63, 89), or interdigitate, i.e. with interlocking lobes (e.g. figs 16, 46). Tubercles are actually hollow extensions of the periclinal walls but, for ease and consistency in describing the broad range of tubercular projections involved, they are presented here as independent bodies arising from the walls.

1. *Nymphoides aurantiaca*: (87 collections seen; 8 SEM) Figs 1-5.

Peak ornamentation: Seed body near-globose but very slightly laterally compressed, dark grey-black, 1.45-2.4 mm long, 1.4-2.2 mm wide, 1.125-1.65(-1.9) mm thick. Hilum within a short circular, projection which bears from around its whole perimeter a hard membranous scale appressed to the seed, occasionally the scale absent from a small portion of the perimeter; scale usually oblique, often much longer on one side and reducing to very short or absent on the opposite side, less usually more or less uniformly circular. Periclinal walls with pentagonal or hexagonal margins although the margins are obscured in mature seeds by a dense covering of tubercles. Tubercles are broad-based and basally appressed, each arising singly from the whole wall surface; they are of two kinds, either strongly tapered upwards to a narrowly obtuse apex and to about 85-100(-140) µm long or truncated at about half to two-thirds that length and with broadly obtuse apices. Only tubercles of a single kind have been found on any one seed.

N. aurantiaca is readily identifiable by the seed surface ornamentation, large seed size, and the scale, the scale being unique within the genus.

Variation: The scale varies considerably in size, but there is apparently no linkage of this variation to geographical distribution. For example, both the largest and the smallest scales known occur in northern Western Australia. The largest scale seen on any seed is from the Mitchell Plateau, Kimberleys, Western Australia (*Kenneally 4758*) where the



Figures 1-5. *Nymphoides aurantiaca*; **1** Lateral view of seed with long-tapered tubercles, the scale at left x 20; **2** Lateral view of oblique scale on seed with broad obtuse tubercles x 100; **3** broad obtuse tubercles x 300; **4** long-tapered tubercles x 305; **5** immature seed showing pitted surface, inverted to partly extruded tubercles, and margins of periclinal cell walls x 875 (**1** from *Aston 1979*; **2, 3** from *Lazarides and Adams 309*; **4** from *Brass 19702*; **5** from *Gill/McKean B423*).

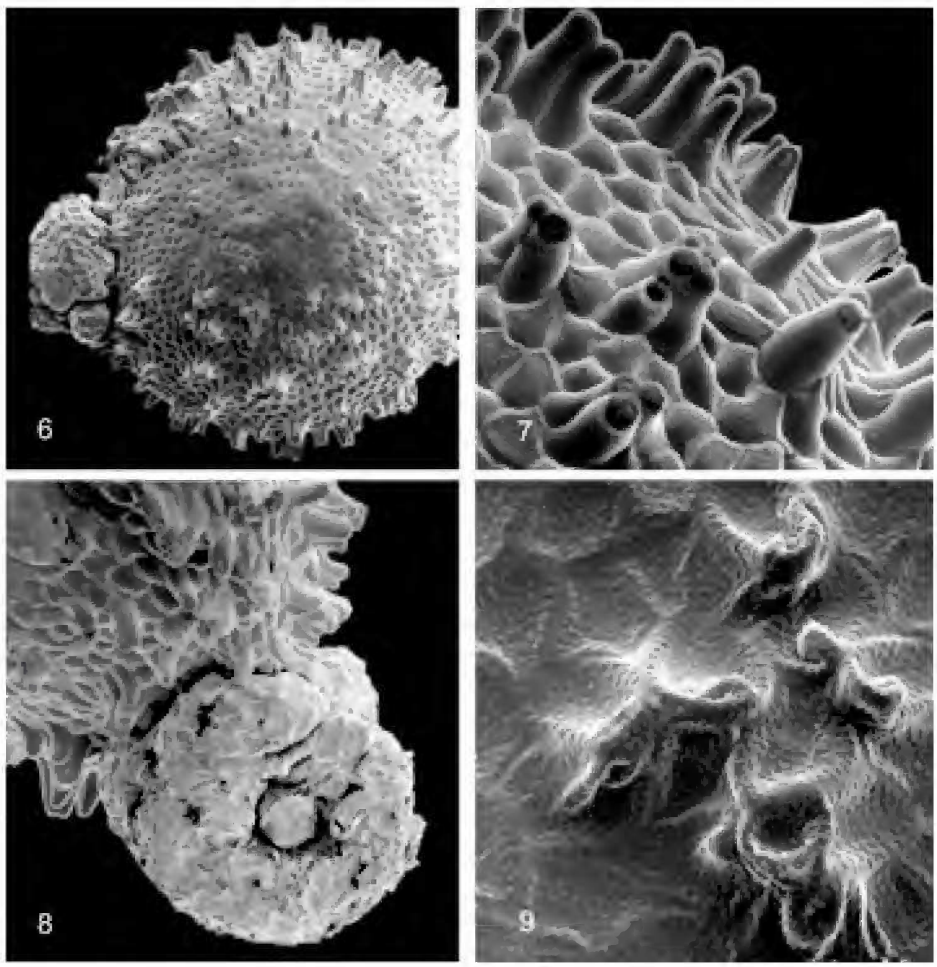
longest side of the scale is about three-quarters of the seed length. Scales at the other extreme of size are reduced to a short, more-or-less inconspicuous membrane only about one-eleventh of the seed length (e.g. *Morton 603*, Weipa, Cape York Peninsula, Queensland; *Beauglehole 52144*, Kimberley district, W.A.). In most populations throughout the Australian range of the species the scales are one-quarter or less of the seed length, but scales to one-third, and sometimes to one-half, seed length are frequent. Ten extra-Australian collections from New Guinea, Sri Lanka, the Moluccas and Thailand which I examined by SEM all had scales which were less than, or rarely one-sixth of, the seed length.

Seeds with the long-tapered tubercles occur in widespread populations throughout northern Australia whereas those with the broadly obtuse tubercles have only been seen from limited areas of the northern Northern Territory. Most collections of the latter seed type come from the area of the South and East Alligator River and their tributary systems, ranging from near Munmarlary, Oenpelli and Nabarlek south through Mudginberri and Jabiru to around Nourlangie (e.g. *Jacobs 1804*; *Lazarides & Adams 309*, figs 2, 3). Other areas from which obtuse-tubercled seeds have been seen are near Daly River (*Craven 4419*) and around the Adelaide River system at Fogg Dam (e.g. *Jacobs 1765*) and Marrakai (*Cousins 178*).

Immature seeds appear deeply pitted over their surface before the tubercles are extruded (fig. 5).

2. *Nymphoides beaglensis*: (7 collections seen; 2 SEM) Figs 6-9.

Peak ornamentation: Seed body near-globose but slightly to moderately laterally compressed, dark grey-brown-black, 0.75-0.95 mm long, 0.70-0.85 mm wide, 0.55-0.70 mm thick. Hilum within a very thick and conspicuous, pale, circular caruncle of many small cells, the circle with an irregular convolution on one side and sometimes somewhat oblique. Epidermal cells of the seed surface all have periclinal walls with pentagonal or hexagonal margins but are otherwise dimorphic. Over much of the seed surface the walls are mildly convex to low-domed, but at intervals of approximately two to four of these convexities the walls form clusters of prominently projecting tubercles. Each cluster consists of one to eight cells, each cell having one simple, thick, tubercle arising from the whole area of the periclinal wall. The tubercles are therefore broad, touching at the base within each cluster, only slightly tapering and a little divergent upwards, broadly obtuse, c. 35-55 μm long and 2.5-3 times as long as wide. Because of the dimorphism of the



Figures 6-9. *Nymphoides beaglensis*; **6** Lateral view of seed, with caruncle at left x 115; **7** portion of seed surface showing cell dimorphism and margins of periclinal cell walls x 405; **8** distal view of caruncle x 215; **9** immature seed showing pitted cells with foveolate surfaces, some with developing tubercles x 720 (**6-8** from *Kenneally* 9451; **9** from *Forrest s.n.*).

epidermal cells, the seed surface appears more or less smooth but with moderately spaced, conspicuous, single- and multi-tuberculate projections.

Variation: The tubercle clusters may be present only on and near the seed edges, but absent from the central areas of the seed faces.

In immature seeds, the convex periclinal walls on mature seeds remain concave so that seeds appear pitted. Tubercles may be only part-formed and semi-immersed within the pits, or non-turgid even when fully extruded. The surfaces of both pits and tubercles are strongly foveolate in *Forrest s.n.*, 1879 (fig. 9).

3. *Nymphoides crenata*: (104 collections seen; 12 SEM) Figs 10-17.

Peak ornamentation: Seed body ellipsoid but strongly laterally compressed, pale straw-coloured to fawn-brown or tan-brown, never black, (0.425-)0.6–1.0(-1.2) mm long, (0.35-) 0.4-0.7(–0.8) mm wide, 0.25-0.55 mm thick. Hilum within a very short, hard, near-basal, ring of the seed body, the ring obliquely circular and forming a minute projection on one side; caruncle absent. Periclinal walls strongly and conspicuously interdigitate, all slightly convex in many populations, giving a more or less smooth seed. In many other populations the walls of some cells each extend into a single central tubercle. Tubercles are thick, broadly obtuse, not touching, from low and domelike to longer and cylindrical, usually 30 μm or less long, rarely to 40 μm; length from less than to 4 times as long as the width, rarely to 6 times the width. Because of the inter-population differences of the shape, placement, and spacing of the tubercles, and their presence or absence, seeds of *N. crenata* are noticeably variable. However, they can be distinguished by the strongly compressed, ellipsoidal, non-carunculate, seed body with hard, near-basal projection.

Variation: Part of the variation in seed ornamentation, shape and size, can be related to geographical distribution, as follows:

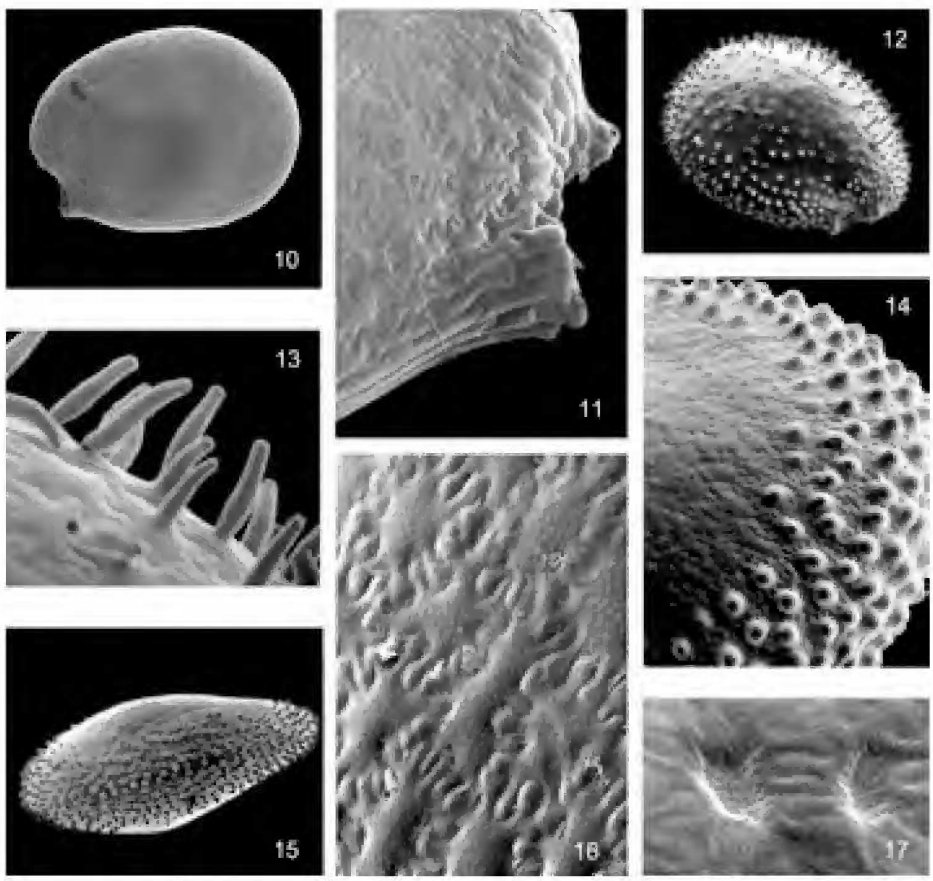
Ornamentation – Mature seeds vary from non-tuberculate and more or less smooth to strongly ornamented with single, non-clustered tubercles. When present, tubercles may occur only on and close to the seed edge, leaving smooth seed faces. They may also extend from the edges over the faces, usually becoming more widely spaced and shorter, or even absent, towards the centre of each face. Edge tubercles occur on all of the edge cells of a seed, whereas face tubercles are usually spaced by one to many non-tuberculate cells. Smooth seeds are prevalent in south-eastern Australia whereas the most highly tuberculate seeds are prevalent throughout tropical areas.

Only smooth seeds have been found on Victorian collections. Most collections from southern Queensland and northern New South Wales between 23° and 32° S latitude and west of 151° E longitude, and also an isolated collection from inland Western Australia, also have smooth seeds (e.g. *Chinnock 808*, Yelma Station, W.A.; *Purdie & Boyland 142*, near Charleville, Qld; *Johnson NSW136695*, near Angledool, N.S.W.). However, a few collections from within this zone have seeds edged with low domes to very short tubercles (e.g. *Wilson & Jacobs 765*, near Pilliga, N.S.W.) and one collection has the seeds shortly tuberculate all over, although very sparsely so on the centre-faces (*Bonney s.n.*, near Jundah, Qld).

Across northern Australia above 18° S. latitude collections show the whole range of seed ornamentation described for the species, without any undoubted correlation of ornamentation with geographical distribution. Although seeds with the longest tubercles all come from five collections from the Northern Territory (e.g. *Byrnes 1817*, fig. 12; *Henshall 3733*, fig. 13) their apparent confinement to the Northern Territory is probably an artefact of the greater number of collections seen from there. Close populations frequently have very different seed ornamentation. For example, *Must 698* (fig. 10) and *N. Byrnes 1817* are from two populations only c. 30 km apart in the vicinity of the Adelaide River, Northern Territory. *Must* has smooth seeds whereas the seeds of the *Byrnes* collection have long tubercles well-distributed over most of their surface. Two collections, *Aston 2275* and *Aston 2279*, from c. 30 km apart in the Normanton area of

Queensland provide another example, seeds of the former having moderately long edge tubercles whereas those of the latter are smooth.

Shape – Four collections from the Cape York and Normanton areas of Queensland (*Aston 2242*, near Laura; *Aston 2269*, Lakefield National Park; *Aston 2280*, near Normanton; *Forster PIF22646*, Bulleringa National Park) and one from the Gulf of Carpentaria region of the Northern Territory (*Thomson 522*, Bing Bong) have more rounded-ellipsoid seeds with mildly to strongly bulged centre-faces. These contrast with the more evenly convex faces of the usual ellipsoid seeds found on other *N. crenata* collections, although some gradations occur. The five collections cited have short to mid-length tubercles on either the seed edges, the edges and side-faces, or over the whole seed surface. Tubercles on seeds of *Forster PIF22646* are short, sometimes only domelike, but are particularly dense, arising from every surface cell.



Figures 10-17. *Nymphoides crenata*; **10** Lateral view of smooth seed × 45; **11** portion of seed showing strongly interdigitate margins of periclinal cell walls and the projection of the seed body which surrounds the hilum × 370; **12** Lateral view of seed with long and widely distributed tubercles × 105; **13** portion of seed with long tubercles × 550; **14** portion of seed with smooth face and low edge tubercles × 275; **15** semi-edge view of seed with smooth centre-face but tuberculate side-faces and edge × 85; **16** surface of mature seed showing strongly interdigitate margins of the convex periclinal cell walls × 1000; **17** immature seed surface showing central foveolate concavity in each periclinal cell wall × 1000; (**10** from *Must 698*; **11** from *Everist 2884*; **12** from *Byrnes 1817*; **13** from *Henshall 3733*; **14** from *Aston 1960*; **15** from *Perry 706*; **16** from *Mckee 8494*; **17** from *Clemens s.n.*, 15 March 1946).

Size – There is an apparent tendency for the smallest seeds to occur in northern tropical Australia and the largest to occur in inland areas of northern New South Wales and southern Queensland.

The smallest seeds measured (< 0.6 mm long) are from six collections from north of 18° S latitude in the Northern Territory and Queensland (e.g. *Byrnes 1817*, Burrell Creek, N.T., fig. 12; *Jacobs 1667*, near Borroloola, N.T.; *Aston 2242*, near Laura, Qld). The largest seeds measured (> 1.0 mm long) are from six collections from southern Queensland and northern New South Wales, between 23° and 32° S latitude and west of 151° E longitude, and from an isolated collection from inland Western Australia (e.g. *Chinnock 808*, Yelma Station, W.A.; *Vogan s.n.*, Upper Mulligan River, Qld; *Boorman NSW136690*, Coolabah, N.S.W.). However, seeds embracing virtually all of the between-extreme lengths of 0.6-1.0 mm occur in all areas throughout the species range. With examination of more collections, the apparent tendency towards a size differential linked to geographical distribution may not be upheld, particularly as the lengths of mature seeds from any one collection frequently vary by up to 0.25 mm (e.g. 0.75-0.95 mm, *Gardner 12220*, Lennard River, W.A.; 0.80-1.05mm, *Johnson & Pedley 61*, Darling Downs, Qld; 0.625-0.825 mm, *Aston 1758*, Yarrawonga, Vic.). Seeds from only one or two capsules from each of 89 collections have been measured.

Immature seeds have concave periclinal walls which appear foveolate (fig. 17).

4. *Nymphoides disperma*: (3 collections seen; 1 SEM) Figs 18-20.

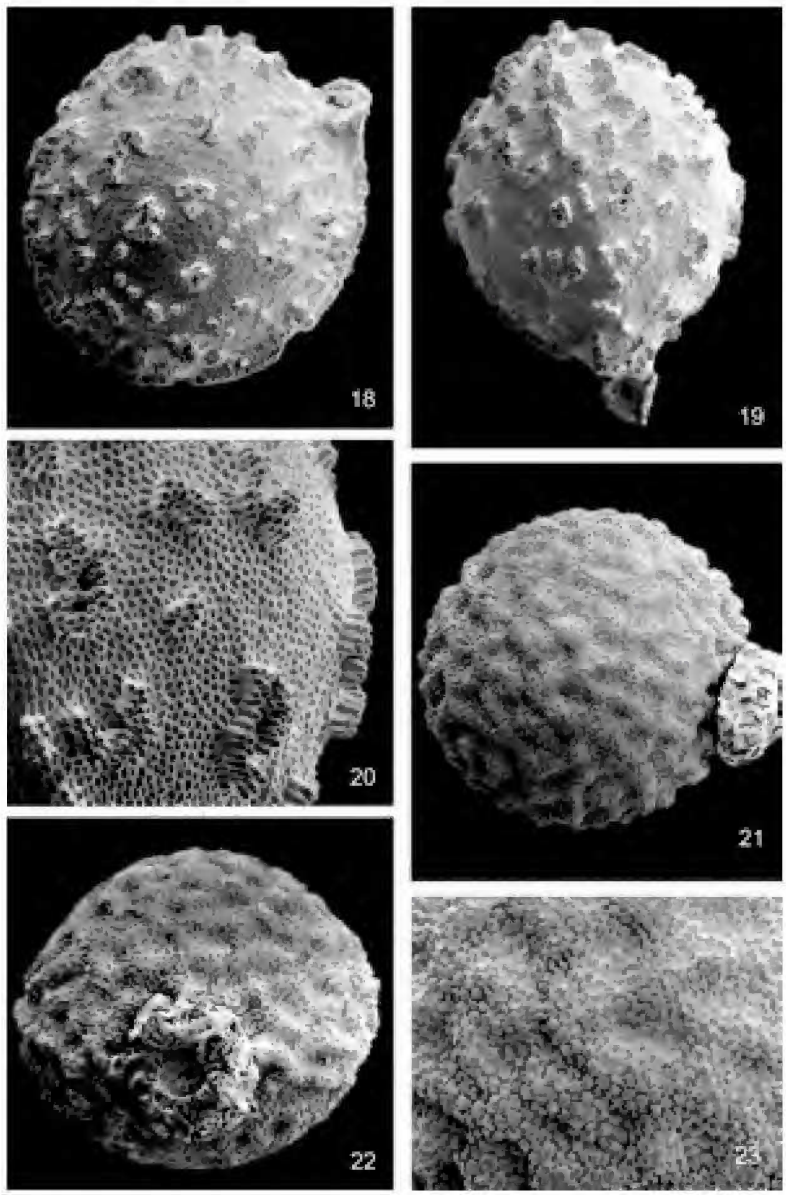
Peak ornamentation: Seed body more or less globose but moderately laterally compressed, straw-coloured (or perhaps finally black), 1.9-2.4 mm long, 1.75-2.3 mm wide, 1.55-1.85 mm thick. Hilum within a very short, thick, oblique projection of the seed body, with most of the perimeter of the projection surrounded by a thin, semi-circular caruncle of many small cells. Periclinal walls with pentagonal or hexagonal margins but otherwise dimorphic. Over much of the seed surface the periclinal walls consist of low convex domes, but at intervals of approximately four to 12 of these domes the walls form clusters of a few to 45 prominently projecting tubercles. Each tubercle arises from the whole area of a periclinal wall. The tubercles are therefore thick, broad and touching at the base, only slightly tapering and a little divergent upwards, broadly obtuse, c. 55-100 μm long and 2.5-5 times as long as wide. Because of the dimorphism of the epidermal cells, the seed surface gives the impression of high, steep-sided plateaus rising abruptly from a uniformly flat plain.

Variation: Seeds of one collection (*George 12508* in part, Prince Regent River Reserve, W.A.) lacked the projecting tubercle clusters but were otherwise comparable with the description given above (see Aston, 1986).

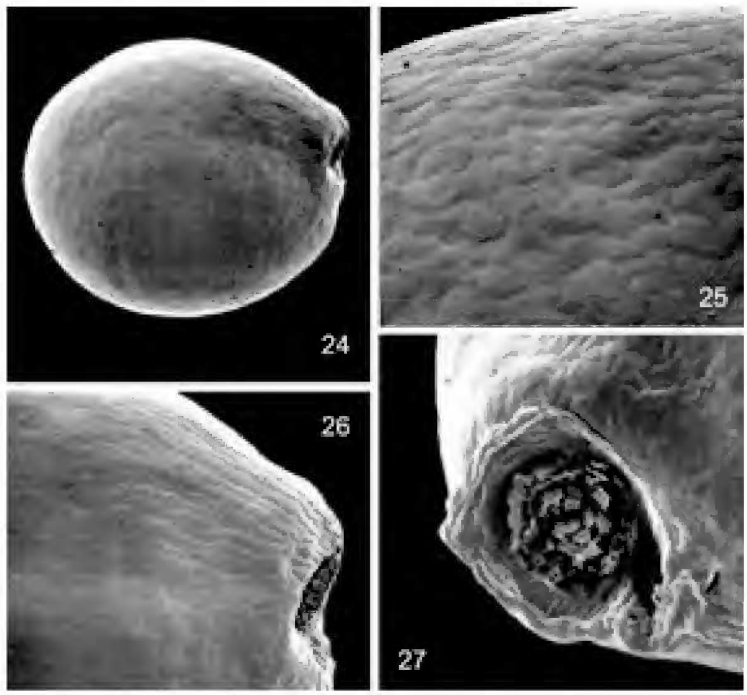
5. *Nymphoides elliptica*: (6 collections seen; 1 SEM) Figs 21-23.

Peak ornamentation: Seed body near-globose but slightly to moderately laterally compressed, dark grey-brown-black, 1.0-1.5 mm long, 1.0-1.3 mm wide, 0.85-1.1 mm thick. Hilum within a pale, circular, moderately thick and prominent, basal caruncle of irregular cells. Periclinal walls with pentagonal or hexagonal margins, each wall bearing a broad-based tubercle arising from virtually all of the wall area. The seed is therefore densely tuberculate with the tubercles often closely appressed. Tubercles are thick, mildly to negligibly tapered upwards, broadly obtuse, often with several minute obtuse micropapillae at their apices, up to 6 μm long and less than twice as long as wide. They vary in length to form a regular, somewhat rugulose, pattern of evenly spaced, more or less circular, depressions separated by reticulate ridging over the whole seed surface. Tubercles of the depressions are shorter than those of the ridging, but the two intergrade gradually. Both the depressions and the ridges are several (c. 6-10) cells wide.

Variation: None observed.



Figures 18-23. *Nymphoides disperma*; **18** Lateral view of seed, the caruncle and hilum at top right x 45; **19** edge view of seed, the caruncle and hilum at bottom x 45; **20** portion of seed surface showing cell dimorphism and margins of periclinal walls x 100 (all from *Forbes 2098*). Nymphoides elliptica; **21** Lateral view of seed, the caruncle at right x 70; **22** edge view of seed, looking on to the caruncle and hilum x 85; **23** portion of seed surface showing depressions, ridging and dense tubercles x 145 (all from *Aston 2260*).



Figures 24-27. *Nymphoides exigua*; **24** Lateral view of whole seed x 35; **25** portion of seed surface showing mildly interdigitate margins of periclinal cell walls x 250; **26** attachment area of seed showing the absence of a caruncle x 80; **27** attachment area with thin caruncular rim x 245 (**24-26** from *Buchanan 2764*; **27** from *Rodway s.n.*, 1896).

6. *Nymphoides exigua*: (4 collections seen; 2 SEM) Figs 24-27.

Peak ornamentation: Seed body rounded-obloid to broad-obloid but strongly laterally compressed, brown-grey, 1.05-1.4 mm long, 0.9-1.1 mm wide, 0.55-0.65 mm thick. Hilum within a small, hard, obliquely circular, near-basal, bulge of the seed body; caruncle absent or represented only by a thin rim or partial rim of cells around the hilum. Periclinal walls with shortly interdigitate margins, each wall slightly convex. Tubercles absent. The seed surface overall appears smooth and shining.

Variation: None observed.

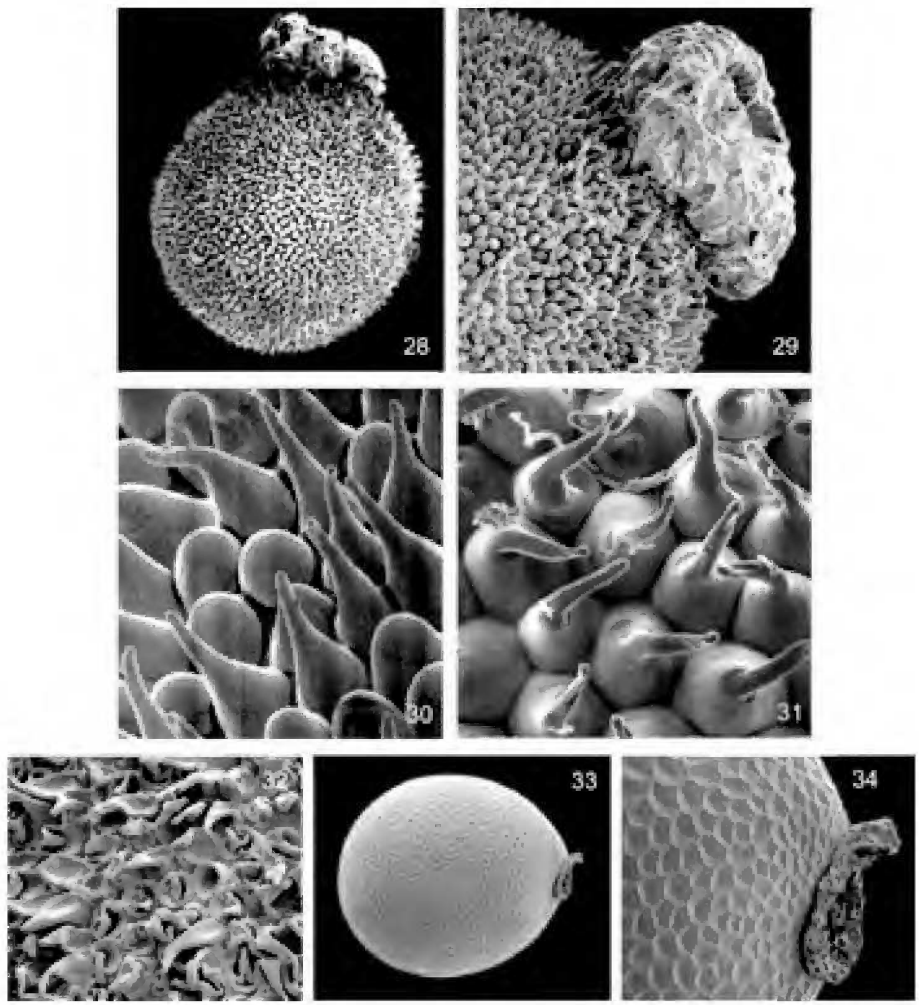
7. *Nymphoides exiliflora*: (41 collections seen; 11 SEM) Figs 28-32.

Peak ornamentation: Seed body ± globular, dark grey-brown to black, (0.4-)0.5-0.8 mm long, (0.4-)0.5-0.75 mm wide, (0.35-)0.45-0.7 mm thick. Hilum within a pale, circular, thick and prominent, basal caruncle of large irregular cells. Periclinal walls with pentagonal or hexagonal margins although the margins are obscured in mature seeds by a dense covering of tubercles. Tubercles broad-based, arising singly from the whole surface of a periclinal wall, and basally appressed; they are of two extremes, the most usual being about 35-50(-70) μm long and bulbous at the base with an abrupt contraction above this into a slender, narrowly obtuse, distal portion. In the less usual extreme, the tubercles are only about half to two-thirds as long, broad throughout, and with a broadly obtuse apex. The dense covering of slender tubercles on most seeds gives a velvety-pubescent appearance to the seed surface.

Variation: The contraction to a slender extremity is less abrupt in the tubercles of some seeds, in which case each tubercle becomes more gently tapered.

All periclinal walls of any seed usually possess the same kind of tubercle, but both distally slender and broad obtuse tubercles have been found intermingled on a few seeds in both Australia and New Guinea (e.g., *Dallachy s.n.*, figs 28, 29; *Ridsdale NGF33531*, fig. 30). Seeds in which all tubercles are tapered occur abundantly throughout the species range, but seeds having only the shorter, broadly obtuse, tubercles have not been found.

Immature seeds appear deeply pitted over their surface before the tubercles are extruded.



Figures 28-34. *Nymphoides exiliflora*; **28** Lateral view of a seed bearing dimorphic tubercles, caruncle at top x 110; **29** portion of seed with dimorphic tubercles, showing latero-distal view of caruncle x 215; **30** surface of seed with both slender-tapered and broad-obtuse tubercles x 1075; **31** bulbous-based, abruptly contracted tubercles x 1150; **32** surface of semi-mature seed showing cell wall margins and developing tubercles x 310 (**28, 29** from Dallachy s.n., [GOET]; **30** from Ridsdale NGF33531; **31** from Dallachy s.n., [MEL]; **32** from Sharpe 1869). *Nymphoides furculifolia*; **33** Lateral view of seed, with caruncle at right x 45; **34** portion of seed showing caruncle and periclinal cell walls x 145 (both from *Lazarides 7645*).

8. *Nymphoides furculifolia*: (33 collections seen; 3 SEM) Figs 33-34.

Peak ornamentation: Seed body near-globose but slightly laterally compressed, dark brown-grey, grey-black or black, 0.55-0.625(-0.75) mm long, 0.50-0.575(-0.65) mm wide, 0.35-0.425(-0.50) mm thick. Hilum within a pale, thin, near-basal, irregularly circular caruncle of small irregular cells. Periclinal walls with pentagonal or hexagonal margins, each wall slightly concave. Tubercles absent. The seed surface overall is glossy and more or less smooth.

Variation: None observed. However, by comparison with the development of seeds of other species it could be expected that the periclinal walls of at least some fully mature seeds may become slightly convex rather than remain concave.

Immature seeds are cream-straw in colour. The most developed show the same size, shape, and surface features as the fully mature black seeds described.

9. *Nymphoides geminata*: (55 collections seen; 19 SEM) Figs 35-43.

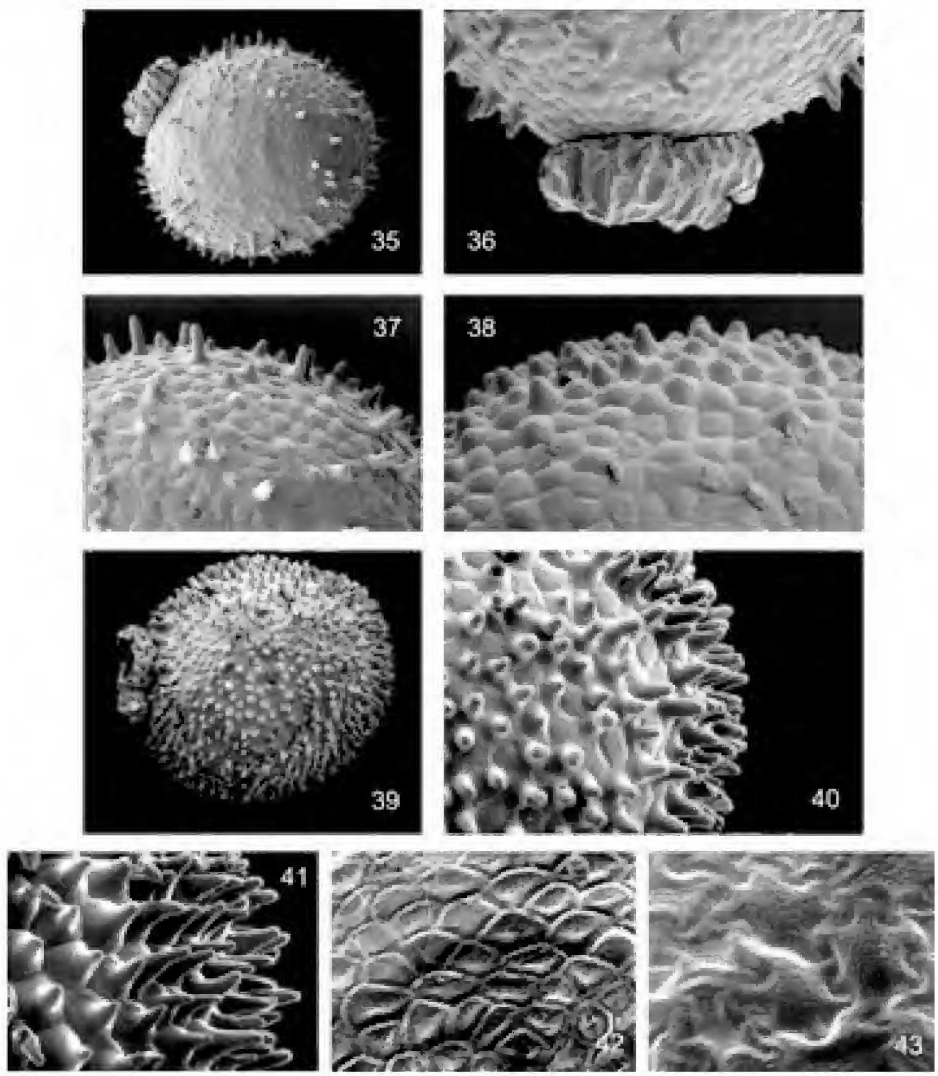
Peak ornamentation: Seed body more or less globular to slightly ellipsoid-globular, slightly to moderately laterally compressed, grey-brown to black, (0.55-)0.6-0.9(-1.2) mm long, (0.5-)0.55-0.75(-0.95) mm wide, (0.4-)0.45-0.65 mm thick. Hilum within a pale, moderately thick and conspicuous, near-basal, circular caruncle of large irregular cells. Periclinal walls with pentagonal or hexagonal margins in most populations, but there are moderately interdigitate margins in some populations (see variation below). Each wall may be slightly convex, or may bear a single tubercle arising centrally from most of the wall area. Tubercles usually non-touching, spaced by one to several cells, often sparse or absent on the seed faces, simple, broadly obtuse, from a low dome or short blunt pyramid up to a moderately broad, slightly tapered tubercle c. 55 μm long and to c. 3 times as long as broad. Seeds may be non-tuberculate and then appear more or less smooth (e.g. *Knoetzsch s.n.*, fig. 42) but they are most commonly tuberculate, with tubercles of all lengths and simple convex periclinal walls included on the same seed (e.g. *Aston 1854*, figs 35-37). More densely tuberculate seeds commonly have tubercles of more or less equal length (e.g. *Aston 1839*, figs 39, 40).

Variation: Seeds from near Tingha, New South Wales (*Aston 1839*, figs 39, 40) and from Glenfield, New South Wales (*McBarron 8556*) are moderately densely tuberculate over their whole surface with even-length, non-appressed tubercles. Many of the tubercles are shortly spaced by non-tuberculate cells. Seeds from two Queensland locations, near Cunnamulla (*Aston s.n.*, Sept. 1969, fig. 41) and near Pentland (*Speck 4602*), are even more densely tuberculate with every cell bearing a broad-based, strongly tapered, prominent tubercle. In the Cunnamulla collection the tubercle bases are somewhat bulbous and appressed so that the seeds are quite similar to those of *N. exiliflora*.

The variation in the length, density and placement of tubercles occurs throughout the geographical range of the species from Queensland to Victoria inclusive. However, I have only seen non-tuberculate seeds (three collections) from Kangaroo Island, South Australia, whereas the only two collections with maximum tubercle density and the most extreme tubercle shape are from the western extremes of the species range in Queensland (see above paragraph).

Fully mature seeds from near Stratford, Victoria (*Aston 1854*, figs 35-37), have moderately interdigitate margins on the periclinal walls of both convex and well-tubercled cells, thereby varying in this character from other Australian collections, including ones from within the same area e.g. Providence Ponds (*Aston 1763A*) and Bengworden (*Aston 1856*). Three collections from New Guinea (*Hoogland & Schodde 7484*, fig. 43; *Walker ANU562*; *Womersley NGF43515*) also have moderately interdigitate margins to the periclinal walls but this may be due to seed immaturity. *Walker ANU562* is very immature, being folded and non-turgid but *Hoogland & Schodde 7484* appears near-mature, with cell walls varying from shallowly concave to low convex.

In immature seeds of Australian collections, the periclinal walls remain inverted so that the seed surface is shallowly to deeply pitted. Wall margins which have not fully lengthened through full cell expansion may have slight curves and appear very mildly interdigitate (e.g., Port Jackson, *F. Bauer s.n.* ?).



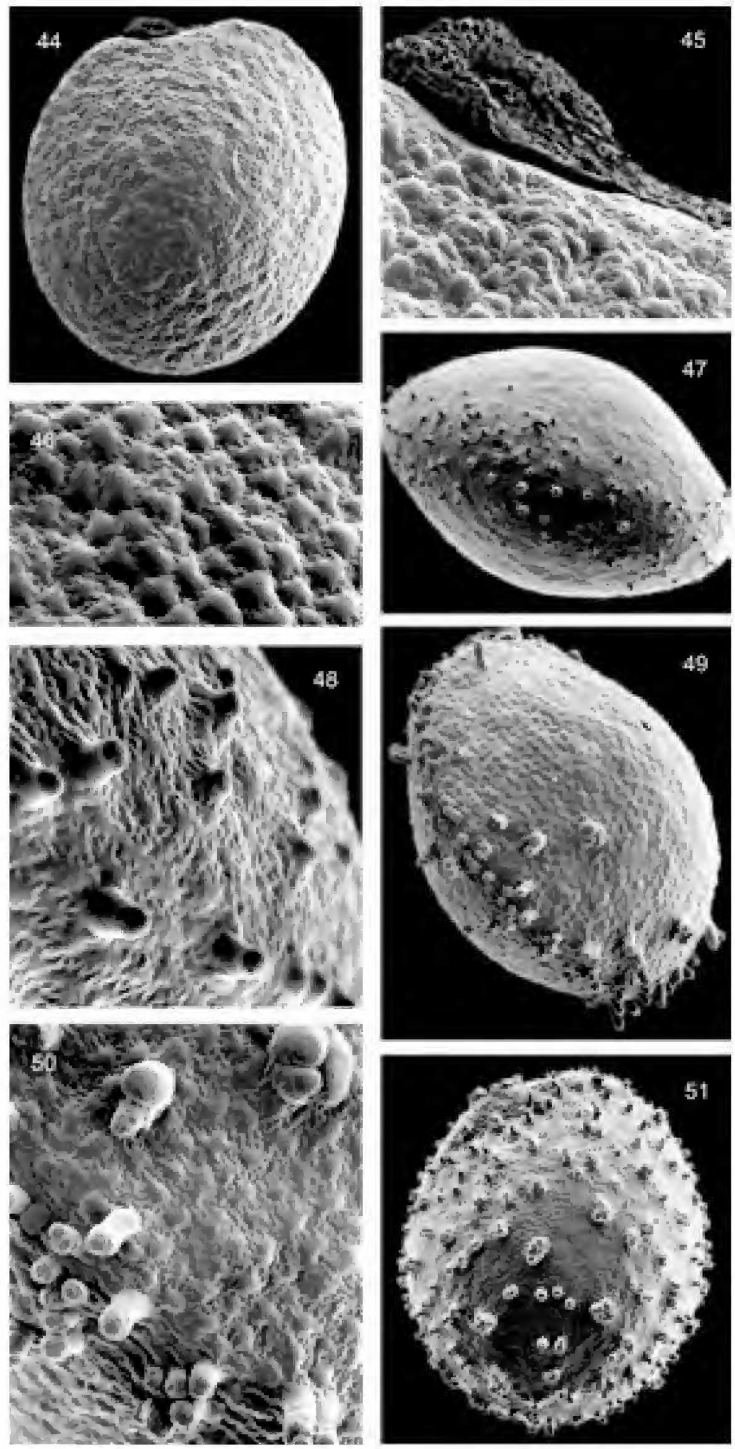
Figures 35-43. *Nymphoides geminata*; **35** Lateral view of seed, with caruncle at left top x 40; **36** portion of seed showing the caruncle x 120; **37** portion of seed showing uneven length tubercles and less usual interdigitate margins of the periclinal cell walls x 100; **38** Portion of seed showing uneven length tubercles and the more usual pentagonal or hexagonal cell margins x 160; **39** Lateral view of seed, with caruncle at left x 40; **40** portion of seed showing even length tubercles and hexagonal or pentagonal cell margins x 120; **41** portion of seed surface showing an even length, unusually bulbous-based, tubercle rising from each periclinal cell wall x 325; **42** seed surface showing pentagonal to hexagonal margins of periclinal cell walls x 320; **43** seed surface showing interdigitate margins x 815 (**35-37** from *Aston 1854*; **38** from *Aston 1840*; **39, 40** from *Aston 1839*; **41** from *Aston*, 26 Sept 1969; **42** from *Knoetzsch*, Jan. 1885; **43** from *Hoogland & Schodde 7484*).

10. Nymphoides indica: (167 collections seen; 14 SEM) Figs 44-58.

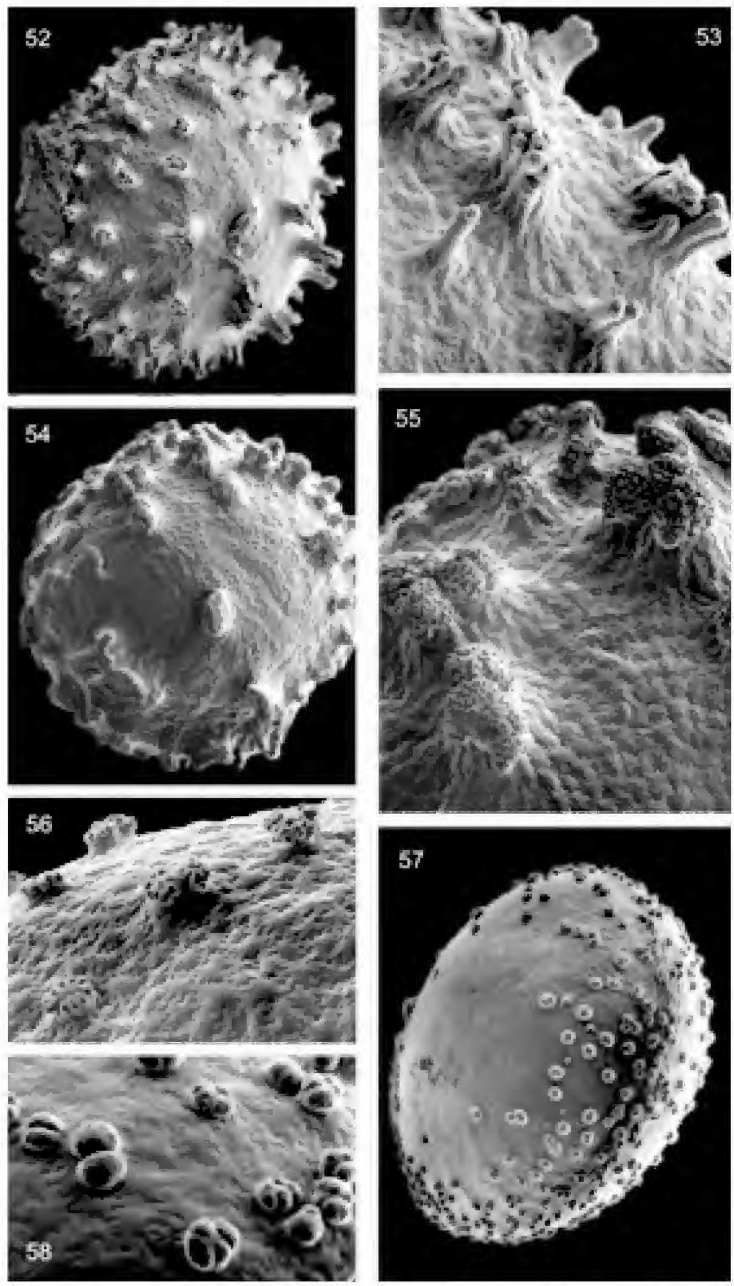
Peak ornamentation: Seed body more or less globose but moderately laterally compressed, cream-straw to fawn-grey to dark grey-brown or black-grey, 0.8-2.1 mm long, (0.725-)0.9-1.7(-1.85) mm wide, (0.5-)0.6-1.2(-1.4) mm thick. Hilum within an evenly circular to oblique, thin and inconspicuous, sometimes apparently absent, basal caruncle, or rarely the caruncle thick and conspicuous. Periclinal walls with strongly interdigitate margins, mostly convex, others variously tuberculate. Tubercles broadly obtuse, varying from solitary to strongly appressed in clusters of 2-11(-20), and from simple to having strongly verrucose extremities. Solitary tubercles are commonly up to c. 96 μm long with the length about four times the width. Tubercle clusters are (20-)50-200(-300) μm long with the length ranging from greater than to lesser than the width. Single tubercles, and/or tubercle clusters, are irregularly spaced over seed surfaces by one to many of the convex-walled cells. Tuberculate seeds therefore appear more or less smooth with spaced tubercles or tuberculate masses. Non-tuberculate seeds have all periclinal walls convex and appear more or less smooth to rugulose throughout.

Variation: *Nymphoides indica* includes a cosmopolitan complex of plants with varied vegetative and reproductive characters which do not lend themselves readily to taxonomic differentiation. The great variability in seed characters illustrates this point. Described below are eight seed variations which encompass the range of seeds which I have seen on Australian material. They indicate morphological progression from non-tubercled to single-tubercled to cluster-tubercled seeds, from simple to distally verrucose tubercles and clusters, and changes in tubercle lengths and surface coverage. Intermediates occur, and some seeds cannot be placed neatly with any one of the forms described. I have not been able to associate the varied seed morphology of Australian populations with any consistent pattern of plant form.

1. Smooth (figs 44-46): seed more or less smooth to rugulose; periclinal walls all convex (*Kenneally 4510*).
2. Single edge tubercles (figs 47, 48): seed as for 1, but with single tubercles 10-30(-60) μm long around edge and side face (*Beauglehole 54910*).
3. Edge clusters (figs 49, 50): seed as for 2, but with some of the tubercles mildly appressed in clusters of 2 to 5 and mildly verrucose at their extremities (*Dixon s.n.*).
4. Overall clusters (fig. 51): seed as for 3, but with the clusters spaced over the whole seed surface, the tubercles mildly adpressed and up to 8 per cluster, 30-50(-80) μm long, each usually slightly broadened toward the summit (*George 15168*).
5. Long-tubercled clusters (figs 52, 53): seed with tubercles (50-)100-210 μm long spaced singly or, most frequently, in clusters of 2-10(-15) over the whole seed surface. Tubercles of each cluster very tightly united along most of their length, their apices verrucose, sometimes divergent. Clusters mostly longer than wide, sometimes appearing spiny when the outer tubercles of the cluster are shorter than the central ones (*Aston 1896*).
6. Long thick clusters (figs 54, 55): seed with all tubercles united into thick clusters 100-250(-300) μm long, with each cluster very strongly verrucose distally. Tubercles fully united and up to 20 (or more) within each cluster. Cluster length mostly more or less equal to the width, but some clusters are narrow and ridgelike (*Aston 2265*).
7. Reduced thick clusters (fig. 56): seed as for 6, but with shorter, fewer-tubercled clusters (30-)40-60(-100) μm long (*Aston 2519*). Most closely related to seed form 4, with intermediates frequent.
8. Very reduced clusters (figs 57, 58): seed as for 7, but with the tubercle clusters even shorter, c. 20-30 μm long, less prominently verrucose, and near-absent from the seed faces (*Edwards s.n.*).



Figures 44-51. *Nymphoides indica*; **44-46** Seed type 1: **44** Lateral view of whole seed × 55; **45** caruncle × 260; **46** seed surface showing interdigitate margins of periclinal cell walls × 290. **47, 48** Seed type 2: **47** Edge view of seed × 95; **48** seed surface at edge showing single tubercles and cell margins × 500. **49, 50** Seed type 3: **49** Semi-edge view of seed × 100; **50** portion of seed surface showing single to few-clustered tubercles with mildly verrucose extremities × 300. **51** Seed type 4: Lateral view of seed × 60.



Figures 52-58. *Nymphoides indica*; **52, 53** Seed type 5: **52** Obliquely lateral view of seed × 60; **53** portion of seed surface showing long, single to clustered, tubercles with more verrucose extremities × 220. **54, 55** Seed type 6: **54** Lateral view of seed × 45; **55** portion of seed surface showing tubercle clusters with strongly verrucose extremities × 145. **56** Seed type 7: portion of seed surface showing shorter, fewer-tubercled clusters × 225. **57, 58** Seed type 8: **57** Semi-edge view of seed × 105; **58** portion of seed surface showing short, almost non-verrucose tubercle clusters × 390. (**44-46** from *Kenneally 4510*; **47, 48** from *Beauglehole 54910*; **49, 50** from *Dixon s.n.*; **51** from *George 15168*; **52, 53** from *Aston 1896*; **54, 55** from *Aston 2265*; **56** from *Aston 2519*; **57, 58** from *Edwards s.n.*

Smooth-seeded collections (89; = 53% of all seeded collections examined) occur through the whole of the species range across northern tropical Australia and down coastal areas of eastern Queensland and north-eastern New South Wales. They were the most prevalent seed form seen in the Northern Territory (37 out of 53 collections; = 69.8%) and Queensland (44 of 76; = 57.9%) and the only form found in the four New South Wales collections. However, smooth-seeded collections from Western Australia were sparse (4 of 34; = 1.2%).

From all the tubercle-seeded collections (78; = 47% of all seeded collections examined), the Kimberley region of Western Australia (30 tubercle-seeded collections seen), the northern Northern Territory (16), and Cape York Peninsula, Queensland (32 from the whole State), each appears to be the centre of development for a different seed form. The most distinctive of these is seed form 6, which has only been seen in ten collections from between 13° and 16° S. latitude on Cape York Peninsula. Seed form 6 and smooth seeds are the only forms which I have seen in collections from the Peninsula. Seed form 5 is most developed in seven collections from the Adelaide River – Kakadu National Park – Katherine area of the Northern Territory, although there are two collections from the Gibb River Road – Durack River area of the Kimberley Region, Western Australia. Seed forms 4 and 7 are connected by intermediates and together form the seed complex which is predominant (15 of 30) in collections from the Kimberley. Forms 2, 3 and 8 also occur in the Kimberley as less frequent gradients of the predominant complex. This whole set of Kimberley gradients also ranges across southern regions of the Gulf of Carpentaria in both the Northern Territory and Queensland, and in the vicinity of Mackay.

Seeds from any one collection have the same seed form but may vary in size of the seed body, e.g. a variation in body length of up to 0.45 mm (1.20-1.65 mm) in *Aston 2536* (Burrells Creek, N.T.). There is no apparent size difference between seeds of different seed forms, with the possible exception of form 6 from Cape York Peninsula. Its seed body lengths of 1.65-2.10 mm average slightly larger than those of other forms but comparatively few seeds have been measured.

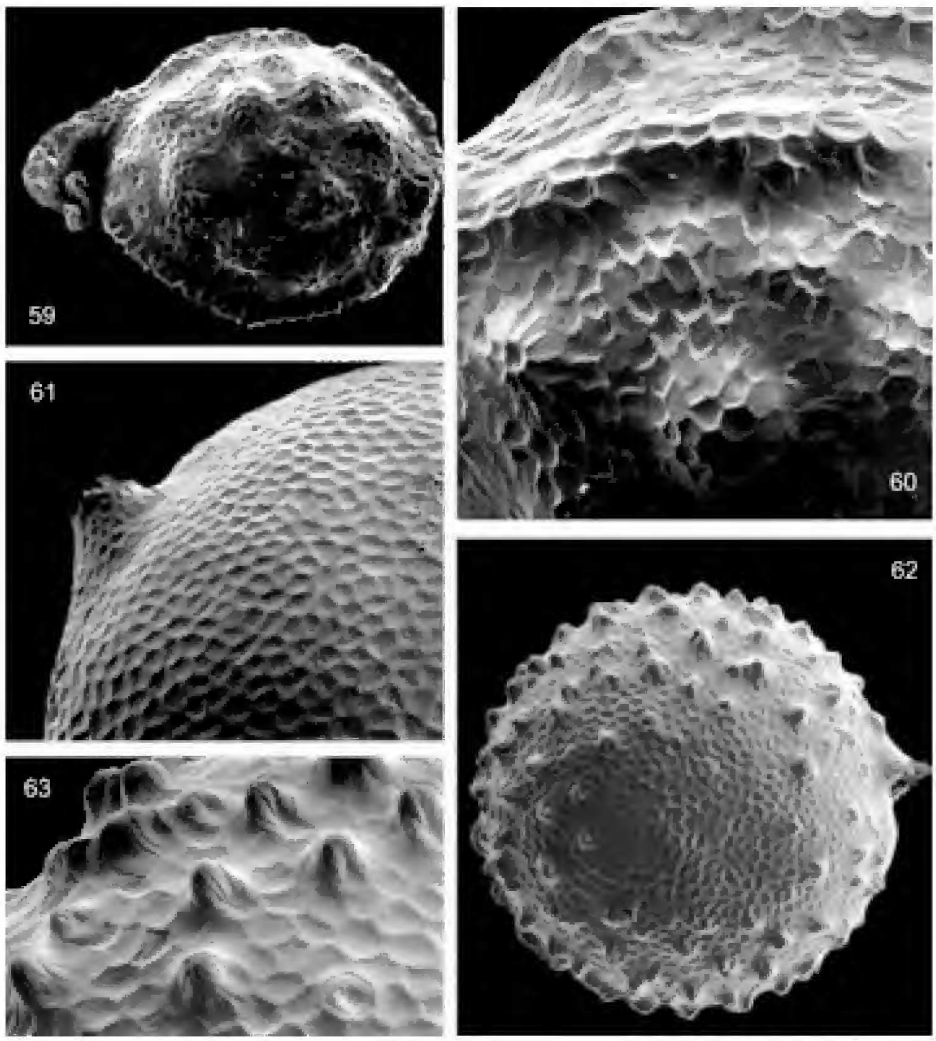
11. *Nymphoides minima*: (68 collections seen; 2 SEM) Figs 59-63.

Peak ornamentation: Seed body near-globose but moderately laterally compressed, cream-straw to fawn-brown or brown-black, 0.5-0.85 mm long, 0.475-0.8 mm wide, (0.275-)0.4-0.6 mm thick. Hilum within a minute, hard, circular, oblique basal projection of the seed body; projection often obscured by a long, looped or coiled, thick-based funicle which may be almost as long as the seed when stretched out; funicle base may be mistaken for a caruncle when the remainder of the funicle breaks off; funicle sometimes short and straight; caruncle absent. Periclinal walls with conspicuous pentagonal or hexagonal margins, each wall concave or occasionally flat to slightly convex. The whole seed surface undulates to form a number of low, broad, multicelled domes on each face and two closely parallel ridges around the seed edge where the domes become denser and more or less united. Most seeds appear shallowly pitted over their whole surface, including the surfaces of the domes and ridges (e.g. *Adams 1767*, figs 59, 60), but some of the darkest, apparently most mature, seeds have flat to mildly convex periclinal walls (e.g. *Aston 2514*, Prince Regent River, W.A.).

Variation: Seeds may lack any development of the domes and ridges and therefore appear uniformly biconvex and more or less smooth, ornamented only by the shallow concavities of the periclinal walls. Various intermediates between these seeds and the well sculptured "peak" form occur. For example, seeds may be smooth and biconvex with only partly-formed edge ridges (*Byrnes 849*, Humpty Doo road, N.T.); they may lack edge ridges but have the broad spaced domes over their whole surfaces (*Byrnes 886*, Jimmy Creek, N.T.; *Rankin 1187*, Berry Springs, N.T.) or over all but the centre-faces

(*Byrnes 1816*, Reynolds Creek, N.T.). Broad domes may be replaced by one- to few-celled projections which simulate narrowed domes of typical seeds (*Aston 1925*, figs 61-63; *Henshall 3661*, Howard Springs, N.T.). Both intermediate and smooth seeds have been found in the same population (*Aston 1925*).

The 68 seeded collections examined comprised 33 from the northern Northern Territory, 23 from the Kimberley region, Western Australia, and 12 (8 N.T.; 4 W.A.) which duplicated localities represented in the other 56 collections, e.g. there are eight different collections from the Edith Falls, N.T. All collections from any one site displayed the same seed form. All Kimberley collections seen possessed the domed and ridged seeds of the well-sculptured "peak" form described, whereas these were fully developed in only three of the 33 Northern



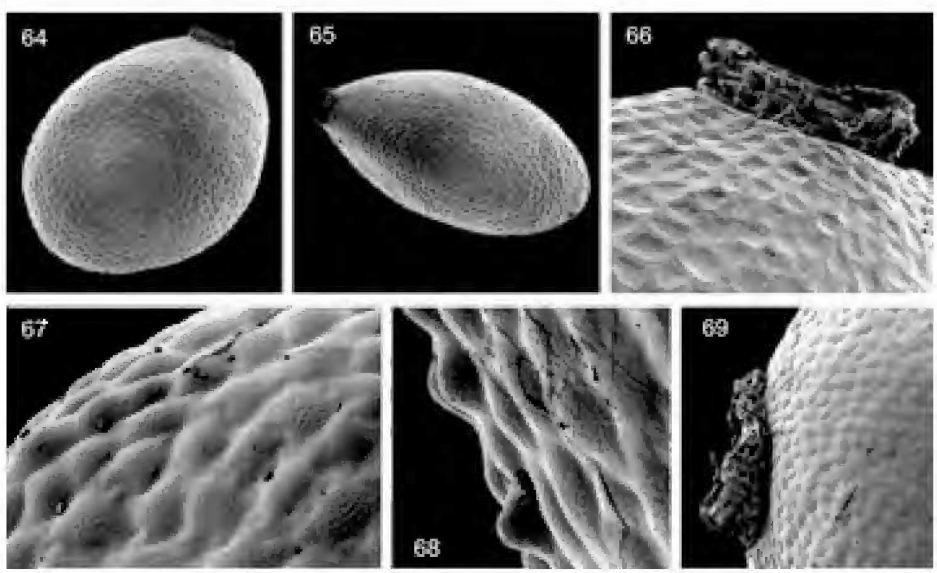
Figures 59-63. *Nymphoides minima*; **59** Lateral view of peak seed form, funicle still attached at left ✕ 105; **60** portion of peak seed showing edge ridges (top) and surface domes ✕ 175; **61** portion of extreme seed form lacking domes or tubercles, with attachment projection at left top ✕ 200; **62** Lateral view of intermediate seed form, with attachment projection at right ✕ 100; **63** portion of intermediate seed showing narrowed domes ✕ 275. (**59, 60** from *Adams 1767*; **61-63** both forms from *Aston 1925*).

Territory locations, namely Allia Creek (*Cowie 4893 & Albrecht*); Edith Falls, (several collections, e.g. *Adams* 1767, figs 59, 60); Upper Fitzmaurice River (*Mueller s.n.*). Of the remaining Northern Territory collections 20 had smooth seeds, or smooth seeds with minute edge sculpturing, and 10 had the various intermediate forms of sculpturing described above. There is therefore a full range of seeds from smooth to the domed/ridged form in the Northern Territory, with apparently a preponderance of smooth or near-smooth seeds. In contrast, only seeds of the domed/ridged form have been found in Western Australian collections.

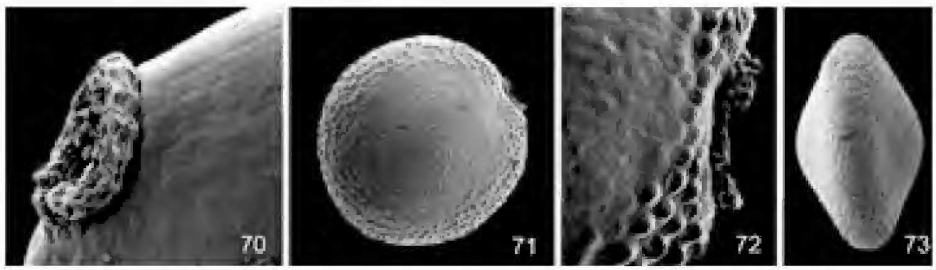
12. *Nymphoides montana*: (31 collections seen; 5 SEM) Figs 64-69.

Peak ornamentation: Seed body ellipsoid but strongly laterally compressed, dark grey-black to black, 1.1-1.55 mm long, 0.825-1.5 mm wide, 0.5-0.725 mm thick. Hilum within a pale, thin, near-basal, circular caruncle of large irregular cells. Periclinal walls with the margins pentagonal or hexagonal, or sometimes tending towards interdigitate, each wall slightly convex. The seed surface overall appears smooth and shining.

Variation: Two collections from the Bentleys Plains, East Gippsland, Victoria (*Beauglehole 36998*, figs 67–69; *Melville 3124*) show a slight tendency towards a tuberculate seed, with the periclinal walls of some spaced cells forming low domes. A few of the walls at the seed edges extend further to form short, tapered, broadly obtuse tubercles about 10-15 µm long, with the width usually about the same as or greater than the length, occasionally only half the length. Two populations near Guyra (*Bell 108*, Billi Bung Lagoon) and Uralla (*Bell s.n.*, Barleyfields Lagoon), both in the Northern Tablelands of New South Wales, have seeds which show the greatest variability known in *N. montana*. These seeds vary from smooth to having the low tubercles moderately densely distributed over the whole seed surface.



Figures 64-69. *Nymphoides montana*; **64** Lateral view of near-mature seed, with caruncle at top × 80; **65** semi-edge view of near-mature seed showing strong lateral compression × 80; **66** portion of near-mature seed showing caruncle and slightly concave periclinal cell walls × 330; **67** portion of mature seed showing convex periclinal cell walls × 320; **68** maximum development of tubercle × 415; **69** portion of mature seed with caruncle at left × 90 (**64-66** from *Adams 1678*; **67-69** from *Beauglehole 36998*).



Figures 70-73. *Nymphoides parvifolia*; **70** Caruncle and seed surface of usual biconvex smooth seed x 210; **71** lateral view of less usual seed with periclinal walls of the edge cells forming low domes x 45; **72** portion of seed showing the caruncle and low surface domes x 175; **73** edge view of seed with the maximum mid-face bulge seen x 45. (**70** from *Aston 2250*; **71-73** from *Clarkson 7794*).

In immature seeds, the convex periclinal walls of mature seeds remain concave so that seeds appear shallowly pitted.

13. *Nymphoides parvifolia*: (34 collections seen; 4 SEM) Figs 70-73.

Peak ornamentation: Seed body near-globose but strongly laterally compressed, from biconvex to broadly and mildly bulged mid-face, brown-black to black, 0.5-0.7 mm long, 0.45-0.675 mm wide, 0.275-0.425 mm thick. Hilum within a basal, circular caruncle of irregular small cells, the caruncle ranging from moderately conspicuous to thin and near-absent. Periclinal walls more or less pentagonal to hexagonal but with mildly interdigitate margins, each wall slightly concave or slightly convex. Tubercles absent. The seed surface appears smooth and shining.

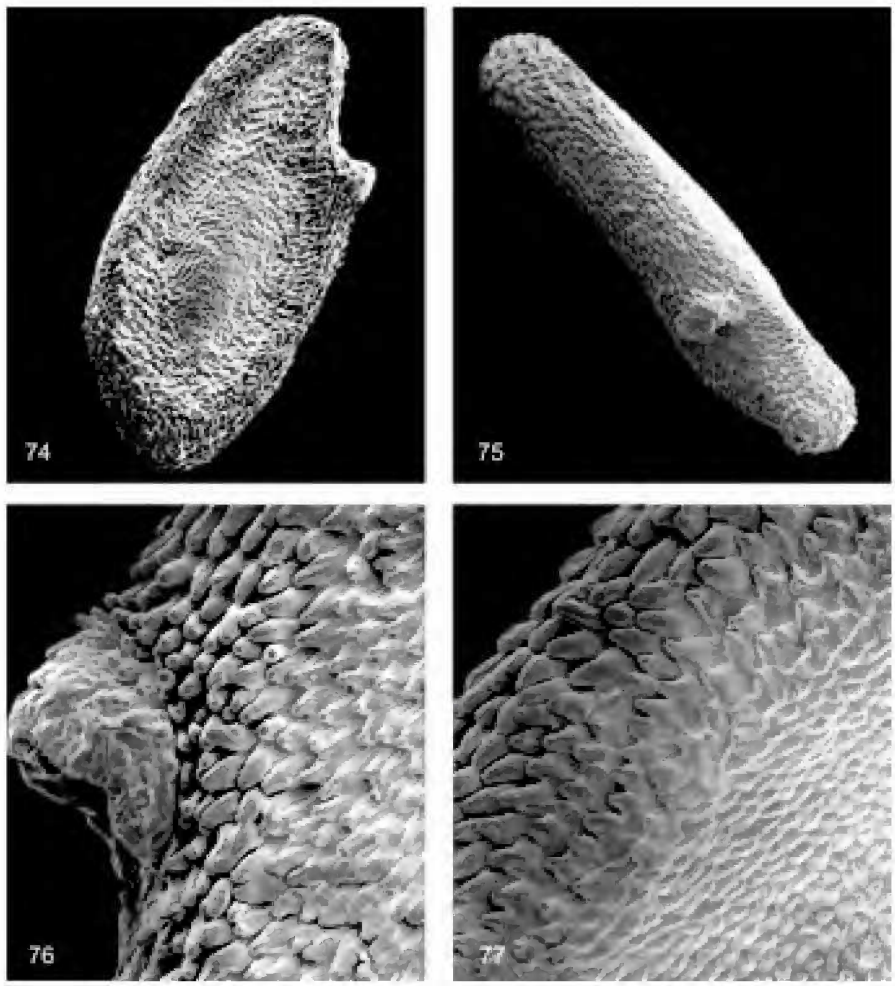
Variation: In a population from Saibai Island [Torres Strait], Queensland (*Clarkson 7794*, figs 71-73) the cells on and close to the seed edge have more pronounced convex periclinal walls, with each wall forming a broad, more or less semicircular dome.

Seeds with unusually large, oblique, conspicuous caruncles which may be 0.14 mm thick at their longest point occur in a collection from the Reynolds River floodplain, Northern Territory (*Cowie 1073*). However, seeds from a second collection from the same vicinity (*Cowie 1080*) possess the usual thinner and non-oblique caruncles.

14. *Nymphoides planosperma*: (5 collections seen; 1 SEM) Figs 74-77.

Peak ornamentation: Seed body narrow-ellipsoid, strongly laterally compressed, black, (1-)1.4-2.25 mm long, (0.5-)0.8-1.05 mm wide, (0.35-)0.45-0.6 mm thick. Hilum within a pale, semicircular, moderately thick caruncle of small irregular cells positioned on the seed edge about one-third of the seed length above the base. Periclinal walls with pentagonal or hexagonal margins. The central area of each seed face is more or less smooth and glossy, somewhat flat to distinctly convex, and has cells with slightly convex to slightly concave periclinal walls. The seed edge is prominently and densely tuberculate, with one broad-based tubercle arising from the whole width of each periclinal wall. Tubercles are regularly tapered upwards, obtuse, directed perpendicularly or slanted unidirectionally toward the seed base, c. 50-65 μm long and more or less twice as long as wide; they reduce in size toward the edge of the non-tuberculate centre-faces. The seed therefore has a distinctive, tuberculate, thickened perimeter strongly contrasting with the comparatively smooth centre-faces. Overall, it appears more or less flat, to flat but centrally bulged, according to the degree of convexity of the centre-faces.

Variation: The tubercles may fail to develop, leaving narrow-ellipsoid, black, glossy, biconvex, more or less smooth seeds, with all cell ornamentation resembling that of the



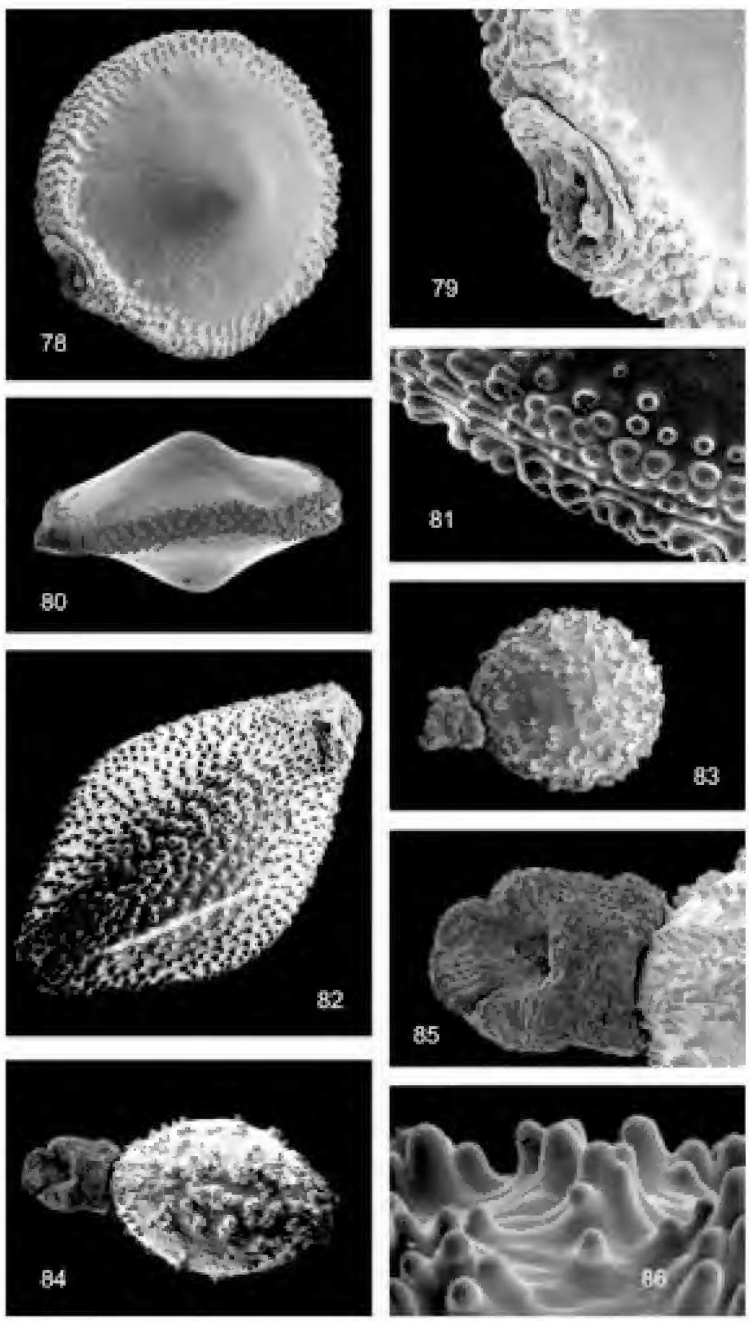
Figures 74-77. *Nymphoides planosperma*; **74** Lateral view of seed x 50; **75** edge view of seed x 50; **76** portion of seed showing the semicircular caruncle x 200; **77** portion of seed showing perimeter tubercles (left) grading to face cells (right) x 200 (all from *Craven 6607*).

seed faces (e.g. *Sanderson & Waterhouse UNSW9634*, Jabiluka Outlier, [between Jabiru and Oenpelli] N.T.). Populations with fully-ornamented seeds (e.g. *Sanderson & Waterhouse UNSW9635*) may exist close to those with smooth seeds. Both these collections were gathered in the same area on the same day but from different pools.

Seed from *Craven 6607* (figs 74-77) is possibly not fully mature. It has fully developed edge tubercles but only moderately developed centre-faces. Seeds from other collections have the centre-faces a little more bulged, with slightly convex rather than concave periclinal walls.

15. *Nymphoides quadriloba*: (48 collections seen: 11 W.A., 30 N.T., 7 Qld; 14 SEM) Figs 78-86.

Two different seed forms of *N. quadriloba*, Typical and Carpentaria, were informally recognised and briefly discussed by Aston (1982). At the same time populations from the



Figures 78-86. *Nymphoides quadriloba*; **78-81** Typical seed: **78** Oblique lateral view of typical seed showing pronounced centre-face bulge and edge tubercles x 100; **79** portion of typical seed showing the caruncle x 280; **80** edge view of typical seed showing the pronounced bulge of centre face x 110; **81** edge of typical seed showing the rectangular cell margins x 335; **82** Carpentaria seed: edge view showing spaced tubercles throughout and the lack of an abrupt central face bulge x 145. **83-86** Kimberley seed: **83** whole seed, face view x 35; **84** whole seed, edge view x 45; **85** caruncle, edge view x 110; **86** portion of seed showing unitubercled to multituberculed projections x 285. (**78, 79** from *Lazarides & Adams 122*; **80, 81** from *Chippendale 7697*; **82** from *Henshall 1938*; **83-86** from *Cowie 4390*).

Kimberley with a third seed form were tentatively placed in the species. I now consider that all three forms are conspecific, and their distinctions and gradations are detailed here.
Peak ornamentations: Typical seeds: [Darwin-Daly River-Katherine-East Alligator River area of the northern Northern Territory and an outlying collection from eastern Arnhem Land (*Cowie 6624 & Bokarra*, Cato River)]: Seed body near-globose but moderately laterally compressed with a pronounced central bulge from each of the faces, cream-straw to brown-black or black, 0.67-1.02 mm long, 0.6-0.95 mm wide, 0.35-0.57 mm thick. Hilum within a thin, circular, basal caruncle of small cells. Periclinal walls mildly interdigitate over the seed faces, the walls becoming more pentagonal or hexagonal near the seed edge and sometimes more or less rectangular over the edge. The walls are dimorphic, being slightly concave to slightly convex over the seed faces, but each produced into a short tubercle at and close to the seed edge. Tubercles smooth, short, thick, only slightly tapered, broad-based and broadly obtuse, c. 15-25 μm long and two or less times as long as wide. The thick, outwardly-directed tubercles occurring densely around the perimeter of the seed form a broad, ± square-cut, tuberculate rim which contrasts strongly with the virtually smooth, prominently bulged, seed faces. Overall, when viewed edge-on, the seed body appears top-shaped or rhomboidal (e.g. *Lazarides & Adams 122*, figs 78, 79; *Chippendale 7697*, figs 80, 81).
Carpentaria seeds: [Corinda-Normanton-Croydon area in the vicinity of the Gulf of Carpentaria, Queensland, and some from the Northern Territory]: Differ from typical seeds by having evenly biconvex instead of centrally-bulged faces, being fully tuberculate, and in having the circular caruncle longer and oblique, i.e. longer overall but even more so on one side (e.g. *Carolin 9104*, Corinda Lagoon, Qld.; *Henshall 1938*, Mary River, N.T., fig. 82). The tubercles are similar in shape to those described above but arise singly from each cell of the whole seed body so that it is covered with moderately spaced, short, thick tubercles. Maximum spacing between tubercles over the central areas of the seed faces is about 1–3 times the width of a tubercle, but decreases towards the edges where many of the tubercles may be touching (e.g. *Henshall 1938*).
Kimberley seeds: [Kimberley district of Western Australia]: Similar to Carpentaria seeds in being evenly biconvex with a long and oblique caruncle. However, the caruncle is usually about twice as long as that of Queensland seeds, with the diameter more or less equal to the greatest length. The largest caruncles seen measure c. 0.1-0.2 mm long at their shortest point and c. 0.175-0.325 mm at their longest point. The most extreme Kimberley seeds (e.g. *Cowie 4390*, Beverley Springs Station, figs 83-86; *Main s.n.*, Woorakin Creek) have this large caruncle and a tubercular surface over which the individual periclinal walls on any one seed may variously lack tubercles, possess a typical single tubercle, or be clustered into multitubercled projections. The two to few tubercles within each projection may be united only at the base or over most of their lengths. They are particularly pronounced in seeds of *Chesterfield 275* (Napier Broome Bay), where single tubercles are sparse and the projections are spaced between areas of low non-tuberculate walls. In contrast, seeds of some collections (e.g. *Kenneally 2193*, Lake Gilbert; *Jacobs 4341*, Mt House, E. of Derby; *Beard 6988*, Mitchell Plateau) are, except for their large caruncle, Carpentaria-like with a uniformly tuberculate surface over which each periclinal wall bears a single tubercle.

Variation: Both Typical and Carpentaria seeds may be modified by absence of the tubercles, giving fully-smooth seeds (e.g. Typical: *Byrnes 1818*, Survey Creek, N.T; Carpentaria: *Aston 2273*, Croydon, Qld). They may also vary in the distribution of the tubercles over the seed surface. In seeds with the Typical bulge-faced shape and thin caruncle, the tubercles may extend onto the side faces, rarely also onto the centre faces (*White s.n.*, June 1955, Mary River, N.T.). In seeds with the Carpentaria biconvex shape and thick caruncle, the tubercles may arise from only some of the cells, may occur over a reduced area of the seed surface, or may be absent, i.e. they may be either spaced by several non-tuberculate cells, present only on the edge and side-faces of the seeds, or missing. The seed variations between populations demonstrate morphological gradients between Typical and Carpentaria seeds in shape (bulged centre-faces to evenly biconvex),

the extent of ornamentation (tubercles absent, to edges only, to edge and side-faces, to whole seed surface), and caruncle (thinly circular to thicker oblique).

Although the Typical and Carpentaria seed shapes are not always as distinctive as described for the extremes, a partial geographical gradient between the two is evident. Typical seeds have not been seen on Queensland collections, and the only Northern Territory fully-tuberculate, biconvex, thicker-caruncled seeds seen are from two populations approaching the Gulf of Carpentaria (*Henshall 1567*, Cox River Station; *Leach 609*, Nathan River Station). The latter, depauperate, collection has been cited by Short (2000) as "*Nymphoides* Nathan River entity".

Kimberley seeds may also be modified by the absence of tubercles to give fully-smooth seeds which retain the large caruncle (e.g. *Kenneally 6589*, Mitchell Plateau; *Kenneally 8243*, Kununurra). The periclinal walls on seeds from Kimberley collections therefore display variations from smooth or mildly convex, to unituberculate and distinct, to clustered with the tubercles united into a multituberculate projection. Typical seeds have not been seen on any Kimberley collection.

In a number of Kimberley collections most of the leaf blades are ovate and comparatively narrower than those from the Northern Territory and Queensland (See Aston, 1982, fig. 3). These include the collections cited above for their most extreme seeds (*Cowie 4390; Main s.n.; Chesterfield 275*), two of the collections cited with uniformly tuberculate seeds (*Kenneally 2193*, *Jacobs 4341*), and smooth-seeded collections. Although the ovate leaves and multituberculate seed ornamentation, best combined in *Cowie 4390*, have not been seen from outside of the Kimberley region, there is apparently no clear correlation of leaf, floral, and seed characters which would allow segregation of a separate taxon.

16. *Nymphoides simulans*: (15 collections seen; 2 SEM) Figs 87-89.

Peak ornamentation: Seeds of this entity have the same characteristics as those of *N. spongiosa*, q.v. There is an apparent tendency for seeds to be smaller on average than those of *N. spongiosa* (0.575-0.85 mm long, 35 seeds measured; cf. 0.65-1.10 mm, 118 seeds measured) but measurements overlap.

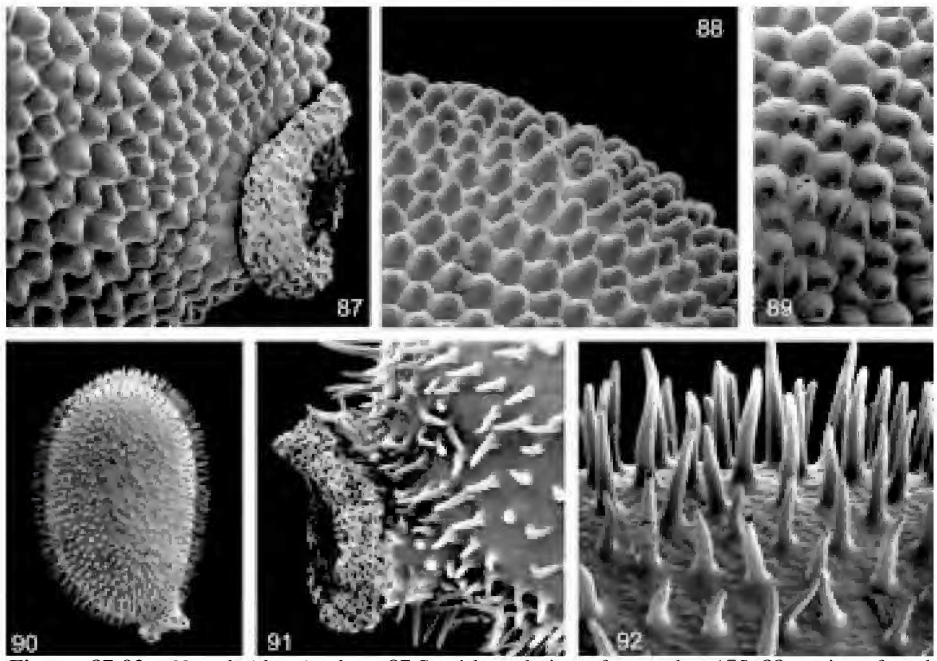
Variation: Variations are the same as those for *N. spongiosa*, e.g. *Craven 3203* (140 km S of Cooktown) has tubercles absent from the centre-faces.

This entity is known chiefly from the Musgrave to Mt Molloy areas of eastern Cape York Peninsula, Queensland, but has also been collected from two locations near the Gulf of Carpentaria at Westmoreland Station, Qld (*Jacobs 1547*, figs 87-89; *Carolin 9203*) and Bing Bong Station, N.T. (*Dunlop 2250*), and from two further locations in the vicinity of the South Alligator River (*Slee et al. 2880*) and East Alligator River, N.T. (*Seddifield s.n.*, DNA 73715). Plants are similar in seeds and leaves to typical *N. spongiosa* of the Northern Territory but differ substantially in several floral characters.

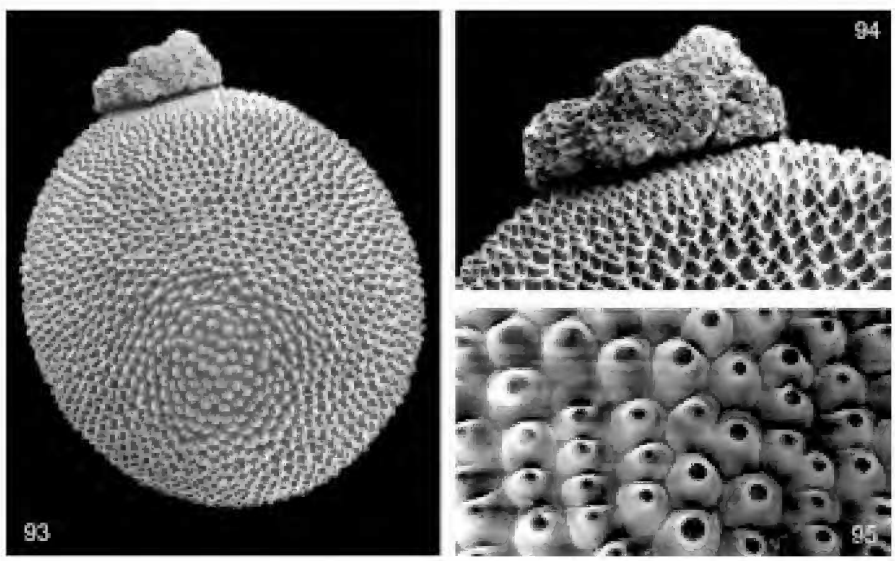
17. *Nymphoides spinulosperma*: (11 collections seen; 1 SEM) Figs 90-92.

Peak ornamentation: Seed body ellipsoid but strongly laterally compressed, black, 1.1-1.5 mm long, 0.8-1.1 mm wide, 0.4-0.5 mm thick. Hilum within a very short, stalk-like, near-basal projection of the cell body, with the end of the projection surrounded by a moderately thick, circular caruncle of numerous small cells. Periclinal walls strongly and conspicuously interdigitate, each bearing a prominent tubercle from its centre, or occasionally tubercles absent from some walls of the seed face. Tubercles smooth, slender, tapered, narrowly obtuse, c. 60-100 µm long and 6 or more times as long as wide. Because of the slender, evenly-spaced tubercles, the whole seed appears moderately densely tuberculate.

Variation: None observed.



Figures 87-92. *Nymphoides simulans*; **87** Semi-lateral view of caruncle x 175; **88** portion of seed surface showing tubercles x 160; **89** vertical view of centre-face of seed surface showing cell periclinal walls x 170 (all from *Jacobs 1547*). *Nymphoides spinulosperma*; **90** Lateral view of seed, with the caruncle at the bottom x 25; **91** portion of seed showing the seed projection with caruncle x 105; **92** portion of seed showing the tubercles and strongly interdigitate margins of the cell walls x 195 (all from *Aston 2870*).



Figures 93-95. *Nymphoides spongiosa*; **93** Lateral view of seed, with caruncle at top x 95; **94** lateral view of caruncle, showing the small caruncular cells x 200; **95** portion of seed surface showing the margins of the cell periclinal walls x 385 (all from *Must 1123*).

18. *Nymphoides spongiosa*: (32 collections seen; 1 SEM) Figs 93-95.

Peak ornamentation: Seed body near-globose but slightly to moderately laterally compressed, cream-straw to light brown-grey or brown-black, 0.65-1.1 mm long, 0.6-0.97 mm wide, 0.35-0.7 mm thick. Hilum within a pale, circular, moderately thick and prominent, (sometimes thin) basal caruncle of small irregular cells. Periclinal walls with pentagonal or hexagonal margins, each wall with a short tubercle arising from the whole wall area. Tubercles broad-based, smooth, strongly tapered upwards, broadly conical but obtuse, c. 15-25 μm long and about as long as wide. The short conical tubercles arising one from each cell give the seed surface a densely granular appearance throughout.

Variation: Tubercles may be more dome-shaped than tapered on some collections (e.g. *Cowie & Cowie 7533*, Howard River Reserve) or may occasionally be confined to the edges and side-faces of seeds, gradually reducing in length from the edges towards the centre-faces which are smooth (e.g. *Lazarides 7639*, vicinity of Nourlangie Creek; *Waterhouse 9649*, near Ja Ja). In immature seeds the periclinal walls are shallowly pitted, each pit consisting of an incipient tubercle not yet extruded (see Aston, 1982).

N. spongiosa is known only from a limited area of the northern Northern Territory, extending east to the East Alligator River and south to about 13° 15' S latitude. See also *N. simulans* above.

19. *Nymphoides subacuta*: (17 collections seen; 2 SEM) Figs 96-97.

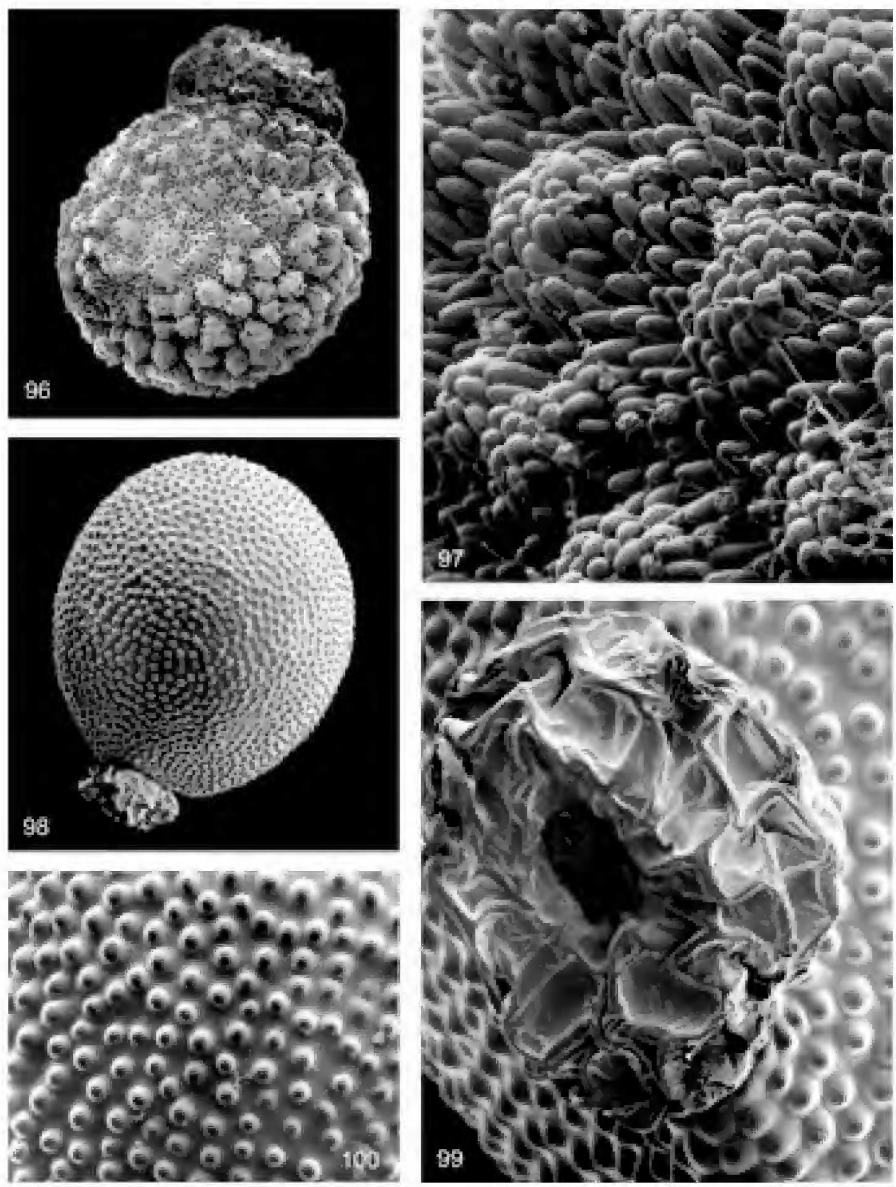
Peak ornamentation: Seed body near-globose but slightly laterally compressed, dark grey-brown-black, 1.4-1.9 mm long, 1.3-1.7 mm wide, 1.1-1.4 mm thick. Hilum within a pale, circular, thick and prominent, basal caruncle of irregular cells. Periclinal wall margins hidden by a dense covering of tubercles. Tubercles one per cell, smooth, broad and tightly appressed at the bases, mildly tapered upwards and broadly obtuse, to c. 70 μm long, the longest ones about three to four times as long as wide. The longest tubercles form dome-like clusters, each cluster consisting of about 20-30 tubercles tightly appressed throughout their length. These clusters are narrowly spaced over the whole seed surface, being separated by and grading into, a reticulate network of lower and narrower inter-dome depressions. This network is covered with shorter tubercles similar to those of the domes but appressed only at their bases. The seed therefore appears to have a regularly domed surface.

Variation: None observed.

20. *Nymphoides triangularis*: (10 collections seen; 1 SEM) Figs 98-100.

Peak ornamentation: Seed body near-globose but slightly to moderately laterally compressed, dark grey-brown-black, 0.45-0.70 mm long, 0.45-0.65 mm wide, 0.25-0.55 mm thick. Hilum within a pale, circular, moderately thick and prominent, basal caruncle of large irregular cells. Periclinal walls with inconspicuous pentagonal or hexagonal margins, each wall with a short, usually dome-like, tubercle arising from most of the wall area. Tubercles broad, smooth, broadly obtuse, c. 6-9 μm long and a little wider than long. Because the tubercles are broad and arise from much of the area of each wall, the tubercles are generally separated from each neighbouring one by less than a tubercle width. The seed surface appears moderately densely granular throughout.

Variation: Tubercles may be present only on and close to the seed edges, gradually diminishing in length from the edge towards the seed face and leaving the face smooth (e.g. *Garnett s.n.,* 5 April 1981, near Edward R. settlement, Cape York, Qld). In *Clarkson 8484 & Neldner*, Wenlock R., Cape York, tubercles are more blunt-conical than dome-like, being fractionally longer than those described, and slightly tapered into a more narrowly obtuse apex.



Figures 96-100. *Nymphoides subacuta*; **96** Semi-lateral view of seed, with caruncle at top x 35; **97** portion of seed surface showing tubercles of the domes and depressions x 260 (both from *Holtze 485*). *Nymphoides triangularis*; **98** Lateral view of seed, the caruncle at bottom x 105; **99** basal portion of seed showing semi-distal view of caruncle surrounding the hilum x 520; **100** portion of seed face showing tubercles x 285 (all from *Aston 2262*).

Discussion

Comparison of mature seeds from Australian collections

The size, shape, ornamentation, caruncle and, to a lesser extent, colour of mature seeds all contribute to the value of seeds in distinguishing Australian species of *Nymphoides*. The following comparisons of these characters should be used in conjunction with the full seed descriptions given under Results and the figures.

Seed size: Seed size is a useful character in distinguishing species, although no species can be identified on seed size alone.

Measurements of the length of the seed body range from 0.4-2.4 mm for all species combined, with a more restricted range for each species. *Nymphoides beaglensis*, *N. exiliflora*, *N. furculifolia*, *N. minima*, *N. parvifolia*, *N. simulans* and *N. triangularis* all have small seeds with the body length consistently less than 1 mm and, except for *N. beaglensis*, 0.85 mm or less. In contrast, the largest seeds occur in *N. aurantiaca*, *N. disperma*, *N. indica*, *N. planosperma* and *N. subacuta*, the only species to have seed bodies which reach 1.6 mm or more long. They may also be shorter, usually no less than 1.4 mm, but as short as 0.8 mm in the exceptionally variable *N. indica*.

The remaining eight species have medium sized seeds with overlapping body lengths in the range of 0.4-1.55 mm. They can be placed in two sub-groups, *N. elliptica*, *N. exigua*, *N. montana* and *N. spinulosperma* (1.0-1.55 mm) contrasting with *N. crenata*, *N. geminata*, *N. quadriloba* and *N. spongiosa* (0.4-1.2 mm). Many seeds of the latter sub-group overlap the range of the consistently small-seeded species.

Seed shape: The length/width ratios of seeds and their degree of lateral compression (thickness) indicate the differences in shape between species. The extreme seed shapes range from narrow-ellipsoid and strongly compressed to near-globular.

Seeds of *N. planosperma* are uniquely shaped in being narrow-ellipsoid, more or less twice as long as wide, and strongly laterally compressed with the width almost twice the thickness. Seeds of *N. crenata*, *N. montana* and *N. spinulosperma* are also strongly laterally compressed, but are broad-ellipsoid with the length only about 1.3 to 1.5 times the width. *Nymphoides exigua* has the same length/width ratio and strong lateral compression as *N. crenata*, *N. montana* and *N. spinulosperma* but is broad-obloid to rounded-obloid rather than ellipsoid.

All other Australian *Nymphoides* species have seeds which are near-globose with the width almost equal to the length. In most of these species the seeds are only slightly to moderately laterally compressed, those of *N. aurantiaca* and *N. exiliflora* being almost totally globular. In contrast, seeds of *N. parvifolia* are the most strongly compressed, with the thickness being only about half to two-thirds of the length and width.

Seeds in some collections of *N. quadriloba* and, to a lesser extent *N. parvifolia*, have centrally bulged faces. These differ from seeds in other collections of the same species, and from those of all other species, which have faces which are evenly curved.

Seed ornamentation: Seeds which are mature and have the most highly developed surface ornamentation, or ornamentations, known for the species concerned, are diagnostic except for distinguishing between *N. spongiosa* and *N. simulans*. Where ornamentations of different species are similar, e.g. as in *N. aurantiaca* and *N. exiliflora*, one or more of the additional characters of seed size, shape and caruncle will allow distinction.

However, ornamentation on even fully mature, turgid, hard, dry, fully-coloured seeds can vary within a species, most notably within *N. indica* and *N. quadriloba*. It may be less prominent because of a reduction in size of the tubercles, a decrease in the number and density of tubercles, or because the tubercles occur over a lesser portion of the seed surface. For example, tubercles commonly develop less in size and density over the central portion of the seed faces compared with their development over the side faces and seed edge (e.g. figs 14, 57). All three reduction features may occur on the one seed, e.g. as in *N. crenata* (fig. 12). In the most extreme reductions, tubercles may be nearly or

entirely absent from mature seeds (e.g. fig. 10). A complex of eight intergrading tubercle variations within *N. indica* (figs 44-58) is described under that species.

The shape of tubercles may also be modified within a species as if tubercle development has ceased before the usual shape has been reached, e.g. as in *N. aurantiaca* (figs 2, 3; cf fig. 4), or in *N. exiliflora* where two tubercle shapes can occur even on the same seed (fig. 30).

The shape of the periclinal walls of mature seeds is generally constant within any one species. In *N. aurantiaca*, *N. beaglensis, N. disperma*, *N. elliptica*, *N. exiliflora*, *N. furculifolia*, *N. minima*, *N. montana*, *N. planosperma*, *N. simulans*, *N. spongiosa* and *N. triangularis* the walls are pentagonal or hexagonal, whereas those of *N. crenata*, *N. indica* and *N. spinulosperma* are strongly interdigitate. *Nymphoides exigua* walls are intermediate between these two extremes, being shortly interdigitate, i.e. more or less shallowly lobed. *Nymphoides quadriloba* walls are usually similar to those of *N. exigua*, although they are sometimes pentagonal and hexagonal at the seed edges. Wall shape in *N. geminata* is generally pentagonal to hexagonal, but rarely shortly interdigitate. It has not been determined for *N. subacuta*.

Periclinal wall shape is best developed over the centre and sides of the seed faces and may also occur over the seed edges. However, quite frequently the edge walls are distorted and differ from those of the centre- and side-faces. Edge distortion is apparently due to a reduced expansion of epidermal cells at seed edges, and becomes more pronounced in immature or less developed seeds.

Caruncle: The hilar region is basal or near-basal in all species of Australian *Nymphoides* except *N. planosperma*, and is accompanied by caruncles or projections of the seed body. These are diagnostic for *N. planosperma* and *N. aurantiaca* and helpful in distinguishing other species.

In *N. aurantiaca* the membranous scale surrounding the hilum is unique, whereas *N. planosperma* is distinguished by the position of the hilum and its semicircular caruncle about one-third of the seed length above the base. Seeds of *N. crenata* and *N. minima* lack caruncles and instead have the hilum within a minute, hard, projection which is continuous with the seed body. In *N. exigua*, the hilum may be within a small circular bulge of the seed body and there may or may not be a thin caruncular rim at the mouth of this bulge. In *N. disperma* there is a short, oblique, projection of the seed body partly edged with a thin caruncle of small cells.

All other species have a circular caruncle composed of cells which are obviously different to the epidermal cells of the seed body. *Nymphoides beaglensis*, *N. exiliflora*, *N. subacuta*, and the Kimberley seeds of *N. quadriloba* have caruncles which are long thick and conspicuous, those of the latter form being exceptionally large (to 0.325 mm long). In contrast, caruncles of *N. furculifolia*, *N. montana* and the Typical seeds of *N. quadriloba* are thin and inconspicuous. Caruncles of *N. indica* (usually thin, rarely thick), *N. parvifolia* (thin to moderately conspicuous), *N. spongiosa* and *N. simulans* (both usually moderately conspicuous, sometimes thin) show variability. In distinguishing species within this group, caruncular size should be used with caution.

Seed colour: Except in *N. crenata*, the darkest colours of fully mature seeds of all Australian *Nymphoides* species range through dark grey-brown to black. Full-sized and expanded seeds which are apparently mature may also be paler grey or straw-coloured in some species.

In *N. crenata* dark seeds have never been seen, all mature seeds being straw-coloured to light tan-brown.

Mature versus immature seeds: It is often difficult to locate capsules with seeds showing the maximum degree of surface ornamentation for the population concerned. Ripening capsules are generally held under water on recurved rotting pedicels which readily break by the time the capsules and seeds are mature. Disturbance usually breaks any tenuous thread still holding a mature capsule, which then sinks, and many collections

therefore lack capsules with fully mature seeds. Before infructescences are disturbed, collectors should search gently for any capsules which are in danger of detachment.

Immature seeds must be viewed with caution, as the degree of development of tubercles and of the periclinal wall shape varies with the degree of seed maturity. Hard, pale, non-turgid seeds approximating the size of mature seeds, will have the same degree of tubercular ornamentation as mature seeds of the same capsule. Even soft (when fresh), half-size, still-developing seeds within the capsule generally give a strong indication of what their mature tubercular ornamentation will be. However, tubercles of immature seeds are often fully or partly inverted within the epidermal cells (fig. 5) before extruding (fig. 32) and inflating at maturity, and immature seeds can therefore give rise to a mistaken interpretation that mature seeds have pitted surfaces.

It is common for the epidermal cells of immature seeds to have sunken, concave, periclinal walls (fig. 9) rather than the raised, convex, walls of associated mature seeds. The shape of periclinal walls is also frequently distorted in immature seeds, particularly at their edges.

Extra-Australian comparisons

There are few published SEM illustrations of seeds of the five non-endemic Australian species from extra-Australian sources, but in a limited study Sivarajan *et al.* (1989) provide figures for Indian collections of *N. aurantiaca, N. indica* and *N. parvifolia*. Their descriptions and figures for *N. aurantiaca* (figs 33-36) agree well with the seed form having a very short scale and short broad obtuse tubercles found in some Australian collections.

For *N. indica*, the illustrations of Sivarajan *et al.* (1989, figs 7-10, 12-14) show similarities to the Australian seed forms numbered 2-4 in the current study whereas the Australian seed form number 1 is shown for a South American collection by Chuang and Ornduff (1992, figs 17 & 18). Sivarajan *et al.* and Chuang and Ornduff examined very few collections. It is possible that enlarged studies would report an increased range of extra-Australian variations for *N. indica* comparable to the large range of variations found in Australian material during the current study. Sivarajan *et al.* noted the need for ".. adequate sampling and more intensive studies on the seed coat patterns of *N. indica* complex" worldwide.

The seed descriptions and figures given by Sivarajan *et al.* (1989, figs 15-17) for *N. parvifolia* in India differ from those reported in the present work. Tubercles on the Indian seeds appear broad, obtuse, and spaced singly or several together over the whole seed surface. In contrast, Australian collections examined had non-tuberculate seeds except in one Torres Strait, Queensland collection. Seeds from this bore short, broad, obtuse, more or less domed tubercles (a little shorter than those on the Indian material) around the edges only. The differences between the Indian and Australian material of *N. parvifolia* fall within the range of seed variations found in other species within Australia (see "Seed ornamentation" under "Discussion" above). They may represent a genuine geographical difference or may simply be due to insufficient sampling.

Conclusions

This study involves the 20 species of *Nymphoides* recognised as occurring in Australia. All of these are native, 15 being endemic and 5 extending outside Australia. The five non-endemic species are *N. aurantiaca*, *N. exiliflora*, *N. geminata*, *N. indica* and *N. parvifolia*.

Morphologically, each species can be placed informally in either a "geminata" or an "indica" group, the two groups differing in flower colour and inflorescence characters (Aston 1982, 1985). The "geminata" group contains 9 species, namely *N. aurantiaca, N. crenata*, *N. disperma*, *N. exigua*, *N. exiliflora, N. geminata, N. montana, N. spinulosperma* and *N. subacuta*. The remaining 11 species are placed in the "indica"

group. The current work demonstrates that neither of these two subgeneric groups can be characterised by any combination of seed characters unique to the group. This is in keeping with Chuang and Ornduff (1992), who found that " ... it would not be possible to characterize each genus of Menyanthaceae by a typical and unique syndrome of morphological and cellular seed structures". Instead, combinations of seed characters, as displayed on fully-ornamented, mature seeds, are diagnostic at species level in Australian species of *Nymphoides*, as they are in the related genus *Villarsia* (Aston, 1969; Chuang and Ornduff, 1992).

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Appendix 1.: *Nymphoides* taxa and Australian collections from which seeds were examined by scanning electron microscopy. Where seed from a collection is illustrated in this paper, the relevant figure number is given in bold at the end of the collection citation. Some New Guinea collections of *N. exiliflora* and *N. geminata* are also included.

1. *N. aurantiaca* (Dalz.) Kuntze: c. 5 km WNW of Cardwell, Qld, Australia. *H.I. Aston 1979* (MEL) (**Fig. 1**); Near Nourlangie Safari Camp, c. 90 miles [145 km] NNE of Pine Creek township, N.T., Australia. *M. Lazarides & L.G. Adams 309* (CANB) (**Figs 2, 3**); Wenlock, Batavia R., Cape York Peninsula, Qld, Australia. *L.J. Brass 19702* (K) (**Fig. 4**); 5 miles [8 km] E. of Humpty Doo, N.T., Australia. *M. Gill (McKean B423)* (L) (**Fig. 5**); Chapman R., Gibb R. to El Questro road, Kimberleys, W.A., Australia. *A.C. Beauglehole 51596* (MEL); Atherton, Qld, Australia. *E.Betche NSW136678* (NSW); 10 km NE of Mudginbarry, N.T., Australia. *S.W.L. Jacobs 1804* (NSW); Mt Molloy, Qld, Australia. *H.S. McKee 9107* (BM).
2. *N. beaglensis* Aston: 8 km E of Beagle Bay, Dampier Peninsula, W.A., Australia. *K. Kenneally 9451* (PERTH, holotype) (**Figs 6-8**); Beagle Bay, W.A., Australia. *A. Forrest s.n.*, 1879 (MEL) (**Fig. 9**).
3. *N. crenata* (F. Muell.) Kuntze: Margaret R. crossing, Deepwater road, N.T., Australia. *J. Must 698* (MEL) (**Fig. 10**); Boatman Station, Maranoa District, Qld., Australia. *S.L. Everist 2884* (K) (**Fig. 11);** Burrell Creek, N.T., Australia. *N. Byrnes 1817* (MEL) (**Fig. 12**); Maryfield Station, Stuart Highway, N.T., Australia. *T.S. Henshall 3733* (DNA) (**Fig. 13**); c. 6 km N of Mareeba, Qld., Australia. *H.I. Aston 1960* (MEL) (**Fig. 14**); James R. crossing on Barkly Highway, N.T., Australia. *R.A. Perry 706* (CANB) (**Fig. 15**); Katherine, N.T., Australia. *H.S. McKee 8494* (K) (**Fig. 16**); Jericho and vicinity, Mitchell District, Qld., Australia. *M.S. Clemens s.n.*, 15 March 1946 (K) (**Fig. 17**); 30 miles [48 km] ENE of El Sherana, N.T., Australia. *L.G.Adams 3070* (CANB); c. 20 miles [32 km] NW of Echuca, Vic., Australia. *H.I. Aston 1701* (MEL); Bing Bong Station, N.T., Australia. *C.R. Dunlop 2248* (DNA); Phillip Creek Station, N.T., Australia. *B.W. Strong 57* (DNA).
4. *N. disperma* Aston: Vansittart Bay, North Kimberley, W.A., Australia. *S.J. Forbes 2098* (PERTH, isotype) (**Figs 18-20**).
5. *N. elliptica* Aston: 10.3 km E of Musgrave, Cape York Peninsula, Qld, Australia. *H.I. Aston 2260* (MEL, holotype) (**Figs 21-23**).
6. *N. exigua* (F. Muell.) Kuntze: Point Hibbs, Tas., Australia. *A.M. Buchanan 2764* (MEL) (**Figs 24-26**); Huonville, Tas., Australia. *L. Rodway s.n.,* Jan. 1896 (MEL) (**Fig. 27**).
7. *N. exiliflora* (F. Muell.) Kuntze: Rockinghams Bay, Qld, Australia. [*J. Dallachy s.n., s. dat.*] (GOET) (**Figs 28, 29**); Weam, Western District, Bensbach Subdistrict, Papua [New Guinea]. *C.E. Ridsdale NGF33531* (L) (**Fig. 30**); Rockingham's Bay, Qld, Australia. *J. Dallachy s.n., s. dat.* (MEL) (**Fig. 31**); 3 km N of Coolum Beach, Qld, Australia. *P. Sharpe 1869* (BRI) (**Fig. 32**); Shoalwater Bay, [Qld, Australia]. *R. Brown s.n., s. dat.* (BM); Hann R., Cape York Peninsula, Qld, Australia. *L.J. Brass 19987* (K); Lawnton, Qld, Australia. *M.S. Clemens 42097* (G); 57 km SSE of Ingham, Qld, Australia. *R. Coveny 6946 & P. Hand* (NSW); Rockingham Bay, Qld., Australia. *J. Dallachy s.n., s. dat.* (K); Kelsey Creek, Qld, Australia. *Rev. N. Michael 945* (BM); Near Bula Village, mouth of Morehead R., Papua [New Guinea]. *R. Pullen 7018* (K).
8. *N. furculifolia* Specht: 13° 12' S., 132° 46' E., N.T., Australia. *M. Lazarides 7645* (CANB) (**Figs 33, 34**); Spencer Range, 26 miles [42 km] E of Oenpelli, N.T., Australia. *L.G. Adams 3000* (CANB); 12° 45' S., 133° 20' E., N.T., Australia. *L.A. Craven 2239* (CANB).
9. *N. geminata* (R.Br.) Kuntze: 4.6 km ENE of Stratford, Vic., Australia. *H.I. Aston 1854* (MEL) (**Figs 35-37**); 3.6 km N of Boonoo Boonoo, N.S.W., Australia. *H.I. Aston 1840* (MEL) (**Fig. 38**); 8.5 km E of Tingha, N.S.W., Australia. *H.I. Aston 1839* (MEL) (**Figs 39, 40**); Between Cunnamulla and Bollon, Qld, Australia. *H.I. Aston s.n.,* 25 Sept. 1969 (MEL) (**Fig. 41**). Boonoo Boonoo via Tenterfield, N.S.W., Australia. *Ch. Knoetzsch s.n.,* Jan. 1885 (MEL) (**Fig. 42**); Yobobos grassland area, Laiagam subdistrict, Western Highlands, New Guinea. *R.D. Hoogland & R. Schodde 7484* (L) (**Fig. 43**); Providence Ponds area, Vic., Australia. *H.I. Aston 1763A* (MEL); 19 km N of Tenterfield, N.S.W., Australia. *H.I. Aston 1841* (MEL); Peecks Road, S. of Bairnsdale, Vic., Australia. *H.I. Aston 1855* (MEL); West of Bengworden, Vic., Australia. *H.I. Aston 1856* (MEL); Port Jackson, N.S.W., Australia. *F. Bauer* [or *R.Brown*] *s.n., s. dat.* (W); Nepean, N.S.W., [Australia]. *R. Brown s.n.*, Dec. 1804. [Type of var. a] (BM); "Nova

Hollandia" [N.S.W.], Australia. *Caley s.n., s. dat.*, (W); Sandy Creek, c. 3 miles [4.8 km] S of Old Bonalbo, N.S.W., Australia. *E.F. Constable NSW66220* (K); Stanthorpe, Qld, Australia. *H.A. Longman s.n.*, 1911 (K); 30 miles [48 km] W of Pentland township, Qld, Australia. *N.H. Speck 4602* (CANB); New England, N.S.W., Australia. [*C. Stuart* ?] (MEL); Sirunki, Western Highlands, New Guinea. *Walker ANU562* (L); Mt Hagen subdistrict, New Guinea. *J. Womersley NGF43515* (L).

10. *N. indica* (L.) Kuntze: Drysdale R. National Park, Kimberley, W.A., Australia. *K.Kenneally 4510* (PERTH) (**Figs 44-46**); Borroloola to Wollogorang road, N.T., Australia. *A.C. Beauglehole 54910* (MEL) (**Figs 47, 48**); Alice R., Qld, Australia. *M. Dixon s.n., s. dat.* (MEL) (**Figs 49, 50**); Traine R., Mt House, Tableland road, W.A., Australia. *A.S. George 15168* (PERTH) (**Fig. 51**); 5–8 km NNE of Katherine, N.T., Australia. *H.I. Aston 1896* (MEL) (**Figs 52, 53**); 5.4 km S of Musgrave, Cape York Peninsula, Qld, Australia. *H.I. Aston 2265* (MEL) (**Figs 54, 55**); Camp Creek, tributary of the Prince Regent R., Kimberley, W.A., Australia. *H.I. Aston 2519* (MEL) (**Fig. 56**); Lennard R., Kimberley, W.A., Australia. *V. Edwards s.n.*, March 1922 (PERTH) (**Figs 57, 58**); 24 km NW of Croydon, Qld, Australia. *H.I. Aston 2272* (MEL); Near Nourlangie Safari Camp, c. 90 miles [145 km] NNE of Pine Creek township, N.T., Australia. *M Lazarides & L.G. Adams 310* (K); Southgate, 8 miles E of Grafton, N.S.W., Australia. *E.C. Macdonald 157* (K); Magella Plain, SW of Cannon Hill, N.T., Australia. *P. Martenz AE259* (CANB); Towards McAdam Range / Arnhem Land [mixed coll.], N.T., Australia. *F.Mueller s.n.*, Oct. 1855 (K); Sideling Creek Dam, Dakabin, near Brisbane, Qld, Australia. *Thorne & Trapnell s.n.*, 10 March 1960 (K).
11. *N. minima* (F. Muell.) Kuntze: Edith Falls, c. 20 miles [32 km] N of Katherine, N.T. Australia. *L.G. Adams 1767* (K) (**Figs 59, 60**); NE of Jimmy's Creek abattoirs, N.T., Australia. *H.I. Aston* 1925 (MEL) (**Figs 61-63**).
12. *N. montana* Aston: Smoker's Gap, Tidbinbilla Range, Paddy's R. district, A.C.T., Australia. *L.G. Adams 1678* (CANB) (**Figs 64-66**); Bentleys Plains, East Gippsland, Vic., Australia. *A.C. Beauglehole 36998* (MEL) (**Figs 67-69**); Camden, County of Cumberland, N.S.W., Australia. *L. Atkinson 11* (MEL); 6 miles [9.6 km] N of Wulgulmerang Post Office, Vic., Australia. *H.I. Aston 1335* (MEL); Dumaresq Dam, c. 12 km NW of Armidale, N.S.W., Australia. *H.I. Aston 1836* (MEL).
13. *N. parvifolia* (Griseb.) Kuntze: Laura to Coen road, Cape York Peninsula, Qld, Australia. *H.I. Aston 2250* (MEL) (**Fig. 70**); Saibai Is., Cook District, Qld, Australia. *J. Clarkson 7794* (MEL) (**Figs 71-73**); 1 mile [1.6 km] S of East Alligator R. crossing, N.T., Australia. *N. Byrnes 841* (MEL); 12° 09' S., 132° 51' E., N.T., Australia. *L.A. Craven 2250* (CANB).
14. *N. planosperma* Aston: c. 22 km NE of Jabiru, N.T., Australia. *L.A. Craven 6607* (MEL, holotype) (**Figs 74-77**).
15. *N. quadriloba* Aston: c. 12 miles [19.3 km] NE of Edith River Siding, N.T., Australia. *M. Lazarides & L.G. Adams 122* (CANB) (**Figs 78, 79**); 2.5 miles [4 km] SW of Fountain Head, N.T., Australia. *G. Chippendale 7697* (K) (**Figs 80, 81**); Mary R., Arnhem Highway, N.T. Australia. *T.S. Henshall 1938* (DNA) (**Fig. 82**); Brolga Swamp, Beverley Springs Station, Kimberley, W.A., Australia. *I.D. Cowie 4390* (DNA) (**Figs 83-86**); c. 2 miles [3.2 km] N of Katherine, N.T., Australia. *L.G. Adams 1747* (K); 5–8 km NNE of Katherine, N.T., Australia. *H.I. Aston 1898* (MEL); c. 41 km NW of Croyden, Qld, Australia. *H.I. Aston 2273* (MEL); Survey Creek, N.T., Australia. *N. Byrnes 1818* (DNA); Napier Broome Bay, Kimberley, W.A., Australia. *E.A. Chesterfield 275* (MEL); 40 km from Normanton on the Croydon road, Qld, Australia. *L.A. Craven 3308A* (MEL); Cox River Station, near Arnold R., N.T., Australia. *T.S. Henshall 1567* (MEL); Lake Gilbert, West Kimberley, W.A., Australia. *K. Kenneally 2193* (PERTH); Near Mitchell Plateau airfield, Kimberley, W.A., Australia. *K. Kenneally 4747* (MEL); Kununurra, Kimberley, W.A., Australia. *K. Kenneally 8243* (PERTH).
16. *N. simulans* Aston [ms, in press, Nov. 2002]: Westmoreland, Qld, Australia. *S.W.L. Jacobs 1547* (NSW) (**Figs 87-89**); E of Musgrave, Cape York Peninsula, Qld, Australia. *H.I. Aston 2261* (MEL).
17. *N. spinulosperma* Aston: 26 km W of St Arnaud, Vic., Australia. *H.I. Aston 2870* (MEL) (**Figs. 90-92**).
18. *N. spongiosa* Aston: Nourlangie Rock area, N.T., Australia. *J. Must 1123* (BRI) (**Figs. 93-95**).
19. *N. subacuta* Aston: Port Darwin, N.T., Australia. *M. Holtze 485* (MEL) (**Figs 96, 97**); 10 miles [16 km] from Darwin, N.T., Australia. *C.E.F. Allen 539* (NSW).
20. *N. triangularis* Aston: 14.8 km E of Musgrave, Cape York Peninsula, Qld, Australia. *H.I. Aston 2262* (MEL, isotype) (**Figs 98-100**).

Appendix 2. Collections cited in this paper, listed in alphabetical order of collector. Identifications are indicated by the species number given in brackets after each collection.

Adams 1678 (12), *Adams 1747* (15), *Adams 1767* (11), *Adams 3000* (8), *Adams 3070* (3), *Allen 539* (19), *Aston 1335* (12), *Aston 1701* (3), *Aston 1758* (3), *Aston 1763A* (9), *Aston 1836* (12), *Aston 1839* (9), *Aston 1840* (9), *Aston 1841* (9), *Aston 1854* (9), *Aston 1855* (9), *Aston 1856* (9), *Aston 1896* (10), *Aston 1898* (15), *Aston 1925* (11), *Aston 1960* (3), *Aston 1979* (1), *Aston 2242* (3), *Aston 2250* (13), *Aston 2260* (5), *Aston 2261* (16), *Aston 2262* (20), *Aston 2265* (10), *Aston 2269* (3), *Aston 2272* (10), *Aston 2273* (15), *Aston 2275* (3), *Aston 2279* (3), *Aston 2280* (3), *Aston 2514* (11), *Aston 2519* (10), *Aston 2536* (10), *Aston 2870* (17), *Aston s.n.* 25.ix.1969 (9), *Atkinson 11* (12), *Bauer* or *Brown s.n. s.dat.* (9), *Beard 6988* (15), *Beauglehole 36998* (12), *Beauglehole 51596* (1), *Beauglehole 52144* (1), *Beauglehole 54910* (10), *Bell 108* (12), *Bell s.n.* 24.ix.1990 (12), *Betche NSW136678* (1), *Bonney s.n.* -.viii.1870 (3), *Boorman NSW136690* (3), *Brass 19702* (1), *Brass 19987* (7), *Brown s.n.* -.xii.1804 (9), *Brown s.n. s.dat.* (7), *Buchanan 2764* (6), *Byrnes 841* (13), *Byrnes 849* (11), *Byrnes 886* (11), *Byrnes 1816* (11), *Byrnes 1817* (3), *Byrnes 1818* (15), *Caley s.n. s.dat.* (9), *Carolin 9104* (15), *Carolin 9203* (16), *Chesterfield 275* (15), *Chinnock 808* (3), *Chippendale 7697* (15), *Clarkson 7794* (13), *Clarkson 8484 & Neldner* (20), *Clemens 42097* (7), *Clemens s.n.* 15.iii.1946 (3), *Constable NSW66220* (9), *Cousins 178* (1), *Coveny 6946 & Hand* (7), *Cowie 1073* (13), *Cowie 1080* (13), *Cowie 4390* (15), *Cowie 4893 & Albrecht* (11), *Cowie 6624 & Bokarra* (15), *Cowie & Cowie 7533* (18), *Craven 2239* (8), *Craven 2250* (13), *Craven 3203* (16), *Craven 3308A* (15), *Craven 4419* (1), *Craven 6607* (14), *Dallachy s.n. s.dat.* (7), *Dixon s.n. s.dat* (10), *Dunlop 2248* (3), *Dunlop 2250* (16), *Edwards s.n.* -.iii.1922 (10), *Everist 2884* (3), *Forbes 2098* (4), *Forster PIF22646* (3), *Forrest s.n.*1879 (2), *Gardner 12220* (3), *Garnett s.n.* 5.iv.1981 (20), *George 12508* in part (4), *George 15168* (10), *Gill (McKean B423)* (1), *Henshall 1567* (15), *Henshall 1938* (15), *Henshall 3661* (11), *Henshall 3733* (3), *Holtze 485* (19), *Hoogland & Schodde 7484* (9), *Jacobs 1547* (16), *Jacobs 1667* (3), *Jacobs 1765* (1), *Jacobs 1804* (1), *Jacobs 4341* (15), *Johnson NSW136695* (3), *Johnson & Pedley 61* (3), *Kenneally 2193* (15), *Kenneally 4510* (10), *Kenneally 4747* (15), *Kenneally 4758* (1), *Kenneally 6589* (15), *Kenneally 8243* (15), *Kenneally 9451* (2), *Knoetzsch s.n.* -.i.1885 (9), *Lazarides 7639* (18), *Lazarides 7645* (8), *Lazarides & Adams 122* (15), *Lazarides & Adams 309* (1), *Lazarides & Adams 310* (10), *Leach 609* (15), *Longman s.n.* 1911 (9), *McBarron 8556* (9), *Macdonald 157* (10), *McKee 8494* (3), *McKee 9107* (1), *Main s.n.* -.viii.1969 (15), *Martenz AE259* (10), *Melville 3124* (12), *Michael 945* (7), *Morton 603* (1), *Mueller s.n.* -.x.1855 (10) (11), *Must 698* (3), *Must 1123* (18), *Perry 706* (3), *Pullen 7018* (7), *Purdie & Boyland 142* (3), *Rankin 1187* (11), *Ridsdale NGF33531* (7), *Rodway s.n.* -.i.1896 (6), *Sanderson & Waterhouse UNSW9634* (14), *Sanderson & Waterhouse UNSW9635* (14), *Seddifield s.n. DNA73715* (16), *Sharpe 1869* (7), *Slee Craven & Brennan 2880* (16), *Speck 4602* (9), *Strong 57* (3), [*C. Stuart* ?] (9), *Thomson 522* (3), *Thorne & Trapnell s.n.* 10.iii.1960 (10), *Vogan s.n.*1889 (3), *Walker ANU562* (9), *Waterhouse 9649* (18), White *s.n.* -.vi.1955 (15), *Wilson & Jacobs 765* (3), *Womersley NGF43515* (9).